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Establishment of native plants on disturbed sites in arctic Alaska

Cargill, Susan Marjorie, Ph.D.

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ESTABLISHMENT OF NATIVE PLANTS ON DISTURBED SITES IN ARCTIC ALASKA

A

THESIS

Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of

Doctor of Philosophy

By

Susan Marjorie Cargill, B.Sc., M.Sc.

Fairbanks, Alaska

September 1988

ESTABLISHMENT OF NATIVE PLANTS

ON DISTURBED SITES IN ARCTIC ALASKA

by

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ABSTRACT

Roads, camps and other structures associated with the Trans-Alaska Pipeline were placed on gravel pads to protect underlying permafrost. Gravel was mined from floodplains, resulting in loss of riparian wildlife habitat. Revegetation of abandoned pads using non-native grasses has been unsuccessful. Native plants might be more persistent and contribute to replacing lost habitat.

The naturally-occurring pioneer community on gravel pads consists mainly of willows Salix alaxensis and S. glauca, fireweed Epilobium latifolium, horsetails Equisetum arvense and legumes in the genera Astragalus, Oxytropis and Hedysarum, all species of riparian gravel bars. Ten years after abandonment mean total cover of native species on 16 gravel pads was only 2.7% and mean number of species per site was 4.4. Distance from riparian seed sources explained 25% and 40% of variation in cover and diversity respectively. Legumes were more restricted to sites near the river than were fireweed and willows.

In the laboratory, no germination of S. alaxensis occurred at water potentials < -0.2 MPa, which probably

occur often on gravel pads. In the field, germination was increased by watering or by a rough surface which provided moister microsites. Growth of seedlings was limited by the supply of mineral nutrients. Survival was high and not limited by availability of water or nutrients.

In the laboratory, few legume seeds germinated at water potentials < -0.5 MPa. In the field, germination was higher on a rough surface which provided moister microsites. Greenhouse experiments indicated that symbiotically-fixed nitrogen contributed significantly to the growth of legume seedlings, especially when availability of mineral N was low. Rhizobia-free legume seedlings transplanted to a gravel pad developed nodules whether or not they were inoculated with rhizobia, but total weight and nodule weight tended to be higher in inoculated seedlings.

Some native plants, primarily riparian species, are capable of establishing and growing on abandoned gravel pads. The low cover and diversity of naturally-colonized sites are attributed to 1) limited dispersal from riparian seed sources, 2) lack of water for germination and 3) lack of nutrients to support growth. Both willows and legumes have promise for use in restoration.

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ACKNOWLEDGMENTS

It is a pleasure to thank my advisor, Dr. Terry Chapin, for so much good advice, so generously given. His contributions to both the planning of my research and the writing of this thesis have proved invaluable. Chapter 1 and combines papers presented by each of us at a conference in 1987. Chapters 2 - 4 report the results of the research I conducted for my dissertation. Dr. Chapin is co-author on each, reflecting his assistance with both research and editing. I am also grateful to my other committee members, Drs. Scott Armbruster, Bonita Neiland, Kent Schwaegerle, Keith Van Cleve and John Zasada for reviewing drafts of chapters, statistical advice and answers to many and varied questions. Mr. Joe Stehlik of the Alaska State Forest Nursery kindly grew the willow seedlings for transplanting. I thank Neil Shishido, Anita Jayaweera and Louise Cargill for their cheerful and competent assistance with field work. Financial support was provided by the U.S. Army Research Office, a Dissertation Improvement Grant (No. DPP8602568) from the National Science Foundation and scholarships from the Natural Sciences and Engineering Research Council (Canada) and the University of Alaska.

INTRODUCTION

During construction of the Trans-Alaska Pipeline System (TAPS), the pipeline right of way, roads, workpads and camps were placed on raised gravel pads up to 1.8m thick, to prevent melting the underlying permafrost. This was effective in preventing thermokarst, but presented new problems related to loss of wildlife habitat and revegetation of the abandoned gravel pads.

In the section of TAPS north of the Brooks Range, most of the gravel was mined from the floodplains of the Sagavanirktok and Atigun Rivers and many of the structures were also placed in the floodplains. This resulted in the destruction of riparian shrub communities which are important to wildlife, including caribou Rangifer tarandus (White & Trudell 1980), muskox Ovibos moschatus (Robus 1981) and moose Alces alces (Mould 1977). Of particular concern was the loss of over 80 ha of tall willow thickets dominated by Salix alaxensis (Anderss.) Cov. S alaxensis is the primary winter browse species for moose (Mould 1977) and is largely restricted to riparian areas.

Once abandoned, the gravel pads proved difficult to revegetate. Most were fertilized and seeded with

non-native grasses, but these revegetation attempts have been largely unsuccessful (Van Cleve & Manthei 1972; Johnson 1981). Revegetation using non-native species has also met with limited success elsewhere in the Arctic (Younkin 1976; Johnson 1981). Contrary to expectations (Lucas 1975), seeding with non-native species has generally failed to facilitate invasion by native species (Johnson 1981; Neiland et al. 1981; Walker et al. 1987).

The difficulties experienced with exotic species have led to considerable interest in alternative approaches to tundra restoration employing native species (Chapin & Chapin 1980, Neiland et al. 1981). Some natural invasion of gravel pads by native plants has occured, but rates are slow and cover and diversity are generally very low (Chapter 2). Establishment of willows is considered particularly desirable because of their importance to wildlife, but attempts at introducing them have not been highly successful. Legumes are important pioneers on riparian gravel bars, and do invade some abandoned gravel pads. They may be useful in restoration because of their capacity for symbiotic N fixation, but there have been no detailed studies of any of the arctic species. Successful use of native plants in restoration will demand better understanding of natural processes of colonization and

succession in the Arctic (Johnson & Van Cleve 1976; Gartner, Chapin & Shaver 1983; Walker et al. 1987).

This thesis consists of 4 chapters, each addressing a different aspect of the problem of restoration of abandoned gravel pads in arctic Alaska. Chapters 2-4 report the results of the research conducted for the dissertation, while Chapter 1 is of a more theoretical nature.

Chapter 1 includes material from papers presented by Dr. Chapin and myself at a conference on "Restoration and Vegetation Succession in Circumpolar Lands" in Reykjavik, Iceland in Sept. 1987. It is a review paper on the problems of restoration in tundra ecosystems in the light of current theory on vegetation succession. This paper is in press in Arctic and Alpine Research.

Chapter 2 deals with natural patterns of colonization of abandoned gravel pads by plants. The objectives of this part of the research were to identify the most important colonizing species, and determine what environmental factors were most important in explaining among-site differences in the extent of natural revegetation.

The research reported in Chapter 3 focused on examining factors limiting the establishment of S. alaxensis on gravel pads. The effects of limited availability of nutrients and water were examined at 3

stages of the life cycle: germination, survival of transplanted seedlings and growth of established seedlings.

Critical stages in the establishment of legumes on gravel pads are likely to include germination, which may be restricted by low soil moisture, and establishment of the rhizobial symbiosis, which may be affected by levels of available N (Skeffington & Bradshaw 1980; Sundstrom et al. 1983) and soil populations of rhizobia (Berg 1974; Townsend 1974; Sundstrom et al 1983). These possibilities were examined in the experiments described in Chapter 4.

Chapters 2, 3 and 4 have been submitted for publication in The Journal of Applied Ecology.

CHAPTER 1

APPLICATION OF SUCCESSIONAL THEORY TO TUNDRA RESTORATION: A REVIEW[1]

ABSTRACT

Life history traits of individual species, competitive interactions and facilitation all contribute to the pattern and rate of succession in tundra ecosystems. An understanding of these natural successional processes will permit the development of effective strategies for restoration of disturbed areas in tundra. In mesic disturbed sites, the soil organic mat remains, providing a source of buried seed and vegetative propagules as well as a store of nutrients. Except where surface erosion is severe, natural succession can proceed quite rapidly, and sowing of exotic grasses is likely to inhibit rather than promote the establishment of native plants. By contrast, revegetation of xeric disturbed sites

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[1]Susan M. Cargill & F. S. Chapin, III, 1988. Arctic and Alpine Research, in press.

is often restricted by inadequate supplies of seed, nitrogen and/or water. Sowing or planting may facilitate the invasion of native plants by increasing nutrient availability, especially if species with symbiotic nitrogen fixation are used. Where erosion hazards are severe, planting may be necessary for engineering reasons, regardless of its effect on the establishment of native plants.

INTRODUCTION

Revegetation is the establishment of plant cover on a disturbed site, where the original vegetation has been partly or completely removed. Restoration has a more restricted meaning: the final objective is a self-sustaining plant community, usually one similar to the predisturbance vegetation. This is essentially a process of vegetation succession, as occurs in nature on disturbed or newly created soils. Therefore, restoration will be most effective if the mechanisms of natural succession are understood, and if this knowledge is applied in the development of methods for restoration. The objectives of this paper are to discuss (1) factors controlling the pattern and rate of successional change and (2) the ways

in which successional theory can be applied to speed ecosystem restoration after disturbance in tundra.

MECHANISMS OF SUCCESSION

Succession has been defined in many different ways; at its simplest it can be taken to mean changes in the plant community on a site over time. Originally, the term applied exclusively to changes in floristics (e.g. Clements 1936), but many recent authors include changes in functional characteristics (Odum 1969). If the site has not previously been occupied by vegetation the succession is termed primary; otherwise it is secondary.

The community present on a site at any point in time, and the patterns of change, are affected by many factors (Fig. 1-1):

1) Life history characteristics of each species, such as dispersal abilities, growth rates, life span and reproductive behavior.

2) Physiological attributes of individual species, such as tolerance to low levels of nutrients, light or water.

3) The ways in which each species modifies the habitat by shading, nutrient and water consumption, deposition of litter, etc.

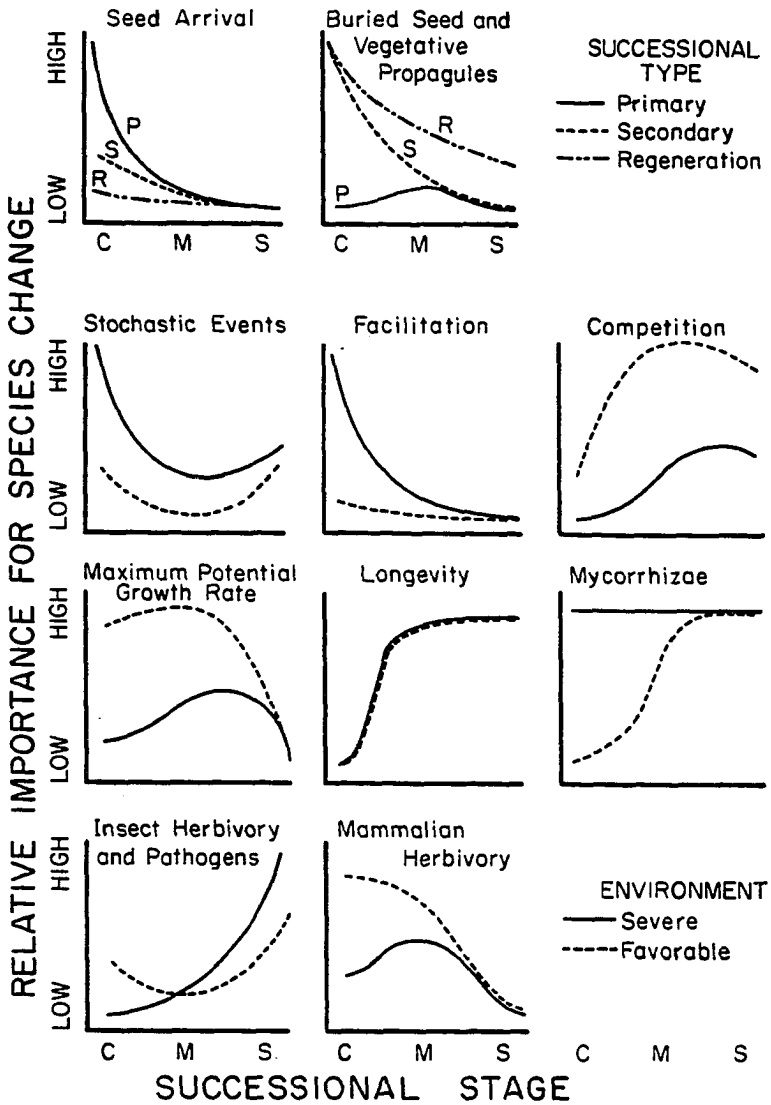

FIG. 1-1. Influence of types of succession upon major successional processes that determine change in species composition during colonization (C), maturation (M) or senescence (S) stages of succession. (From Walker & Chapin 1987).

4) Interactions of the above which determine the competitive and/or mutualistic relationships among species.

The relative importances of these processes can be expected to differ in different successional sequences, and a thorough understanding of any succession will depend on determining how the individual processes are operating. The three contrasting models proposed by Connell & Slatyer (1977) make a useful framework for discussion, although many successional sequences will not be completely explained by any one of the models (McIntosh 1981).

Model 1 - Facilitation. This is the classic model of succession originally proposed by Clements (1936). Change occurs because the early colonizing species alter the environment in ways that gradually make it less favorable for themselves and more favorable for other, later-successional species. The environment changes through succession, and species occur at points in the sequence determined mainly by their physiological adaptations.

Model 2 - Inhibition. Several experimental studies have demonstrated competition between early and late successional species, so that colonizing species inhibit, rather than facilitate, invasion by other species (Keever 1950; McCormick 1977; Hils & Vankat 1982). Later-successional species may assume dominance only after the

death of the pioneer species, which releases them from competitive inhibition.

Model 3 - Tolerance. It has also been observed that late successional species may be present in the early stages of colonization, but not dominate until later because of their slow growth rate (Egler 1954) They survive for long periods as seedlings or small plants, and eventually assume dominance as the early-successional species die. In contrast to model 2, growth of the late-successional species is not increased by removal of the early dominants.

FLOODPLAIN SUCCESSION IN INTERIOR ALASKA

Aspects of all three models of succession are illustrated in a study of seedling establishment during primary succession on the floodplain of the Tanana River in interior Alaska (Walker & Chapin 1986; Walker et al. 1986). Early successional willows (Salix alaxensis and S. interior) and mid-successional poplars (Populus balsamifera) are light-seeded and arrive on uncolonized silt bars in greater abundance than do alder (Alnus tenuifolia) and spruce (Picea glauca). The willows and poplars are also fast-growing and therefore dominate in the early stages. In contrast, spruce is the longest lived

and survives to dominate in the latest successional stages.

The pattern of succession in this system depends on these life history processes (tolerance model), but the rate is modified by both facilitative and competitive interactions. For example, symbiotic bacteria associated with alder fix nitrogen, so nitrogen availability is highest, and seedling growth least nitrogen-limited, in the alder-dominated stage. However, alder also competitively inhibits growth of understory spruce seedlings by shading and root competition. In all successional stages, litter inhibits germination and initial establishment of seedlings. In the short term, these competitive effects outweigh the facilitative effect of increased nitrogen availability.

Herbivory by snowshoe hares and moose is an important factor speeding the elimination of willow from mid-successional alder thickets. Annual variations in snowshoe hare populations strongly influence the rate of succession, as do other stochastic factors such as floods and variation in seed crops. Perhaps the most important conclusion of the study is that succession is the result of many interacting processes (Fig. 1-1) and cannot be adequately described by a single model (Walker & Chapin 1987).

NATURAL SUCCESSION IN THE ARCTIC

The processes that drive succession are likely to differ greatly among different arctic plant communities. In relatively mesic sites such as recently drained lake basins, colonization appears to be limited largely by seed rain, and early colonizers are more likely to inhibit later arrivals by competition than to facilitate their establishment (Billings & Peterson 1980; Peterson 1987). In contrast, soils exposed by the retreat of glaciers contain very little nitrogen, so species with nitrogen-fixing symbionts are important early colonizers, leading to a buildup of soil nitrogen and subsequent community development (Crocker & Major 1955; Viereck 1966; Ugolini 1968). It seems probable, although it has not been experimentally verified, that the effects of these symbiotic nitrogen fixers (Alnus, Dryas drummondii and various legumes) outweigh their competitive interactions with other plants. Succession in arctic riparian areas is similar to that described above for the Tanana River (Bliss & Cantlon 1957). The pattern of succession is largely determined by life history traits. Early colonizers include light-seeded species (Salix alaxensis, S. glauca and Epilobium latifolium) and legumes whose seeds are probably carried by wind and water from nearby

gravel bars (e.g. Astragalus alpinus, Oxytropis maydelliana, and Hedysarum mackenzii) (Robus 1981; Moore 1983). These species are probably relatively short-lived and are eventually replaced by long-lived species such as Dryas integrifolia and Carex aquatilis. Although there have been no experimental studies, we might expect many of these early-successional species to facilitate establishment of later species by stabilization of substrate, and in the case of legumes by symbiotic nitrogen fixation. However, competitive interactions may also be important.

This kind of knowledge about natural successional processes can be used to predict the patterns of recovery following disturbance, and to design restoration projects that will achieve the desired goals. Lacking this basic information on succession, the long-term results of any attempts at restoration are unpredictable.

RESTORATION OF MESIC DISTURBED SITES

In areas of ice-rich permafrost, recovery from disturbance is likely to be very slow, because soils and hydrology are disturbed by thermokarst and erosion. On other mesic sites, recovery is relatively rapid. Soil nutrient and water regimes are relatively favorable for

adapted native species, so seed supply is the most likely limitation to initial colonization. Once the first plants are established, competitive interactions probably outweigh facilitative effects on later-successional species.

These points are clearly illustrated in recovery after blading of tussock tundra, in cases where at least part of the organic mat remains. This soil organic mat contains most of the stored nutrients in tundra (Chapin et al. 1980; Dowding et al. 1981). When the insulative layer of vegetation is removed, the rate of decomposition increases, and the organic mat serves as a slow-release fertilizer, so there is little nutrient limitation to the growth of seedlings (Chapin & Chapin 1980; Gartner et al. 1983).

The organic mat in tussock tundra contains abundant buried seed (McGraw 1980; Roach 1985; Gartner et al. 1986), primarily of the sedges Eriophorum vaginatum and Carex bigelowii. Similarly, the organic mat of coastal wet meadow tundra contains abundant seed of Chrysosplenium tetrandrum (Leck 1980). In tussock tundra, this buried seed is sufficient to completely revegetate the disturbed site (Chester & Shaver 1982; Gartner et al. 1983), so that productivity returns to that of undisturbed tundra within 10 years (Chapin & Chapin 1980).

Because the organic mat contains buried seeds, as well as some living belowground stems of shrubs, this recovery is essentially a secondary successional sequence. Initially, the disturbed sites are dominated by the sedges from the buried seed pool, and some shrubs that sprout from the surviving below-ground stems. Further invasion of shrubs by seed is slow, so at least 50 to 100 years may be required to completely restore the original community. However, this is extremely rapid compared to primary successional processes in tundra (Billings & Peterson 1980; Peterson & Billings 1980; Peterson 1987).

Any attempts to speed up this recovery process, except for soil stabilization, are likely to be counter-productive. In disturbed tussock tundra sites with some remaining organic mat, seeding of native and exotic grasses has either inhibited the growth of sedges establishing from the buried seed pool, or had no effect on them (Chapin & Chapin 1980; Johnson 1987). Because the initial site conditions are suitable for the native sedges, there is little opportunity for facilitation by the sown species, and their effects are mainly competitive. The dense litter which is produced on some seeded sites may also be a barrier to establishment of the sedges (Johnson & Van Cleve 1976).

In cases where there is no buried seed pool, seeding of native species may be desirable. For example when the entire organic mat is removed by blading, few buried seeds remain, and initial seedling establishment is slow, depending entirely upon current seed rain (Gartner et al. 1983). In such cases Calamagrostis canadensis and Arctagrostis latifolia become important (Chapin & Shaver 1981).

It is important to recognize that seeding of exotic grasses may be beneficial for restoration in some cases, despite its inhibitory effects on natural recolonization. This is most likely to be true in areas of ice-rich permafrost (Van Cleve & Manthei 1972) or high winds (Arnalds 1988) where rapid development of cover is important to reduce erosion. The ideal solution may be to sow low densities of exotic grasses that are known to have poor survival or competitive ability in the arctic environment; this could provide initial cover without strongly inhibiting later establishment of native species. The dynamics of such a system would resemble those described in the tolerance model of succession. However, it should be recognized that in many situations where severe thermokarst problems exist, even rapidly-growing plants are unlikely to produce an insulating layer quickly enough to prevent erosion (Hernandez 1973).

RECOVERY OF VEHICLE TRACKS IN TUNDRA

Passage of vehicles over mesic tundra surfaces often increases plant productivity, if the vegetation mat is not greatly disturbed (Hernandez 1973; Wein & Bliss 1973; Chapin & Shaver 1981; Fig. 1-2). This increased productivity is associated primarily with changes in soil environment, e.g. increased bulk density (Gersper & Challinor 1975), radiation absorption, soil temperature and thaw depth (Bliss & Wein 1972; Hernandez 1972; Haag & Bliss 1974; Babb 1977; Chapin & Shaver 1981) and nutrient availability (Challinor & Gersper 1975; Babb 1977; Chapin & Shaver 1981; Fig. 1-2). Where the impact is minor, perhaps a single passage by a vehicle in winter, there may be no long-term changes in thaw, hydrology or vegetation, and the site may return to its original condition within a few years (Webber & Ives 1978; Webber et al. 1980).

At the opposite extreme, thermokarst erosion in areas of ice-rich permafrost, especially following removal of the vegetation and organic mat, may lead to a permanently altered hydrologic regime. The pattern of succession will be strongly influenced by the new abiotic conditions, and may not return to the original community except on the time scale of landscape evolution (hundreds or thousands of years). In some vehicle tracks in tussock

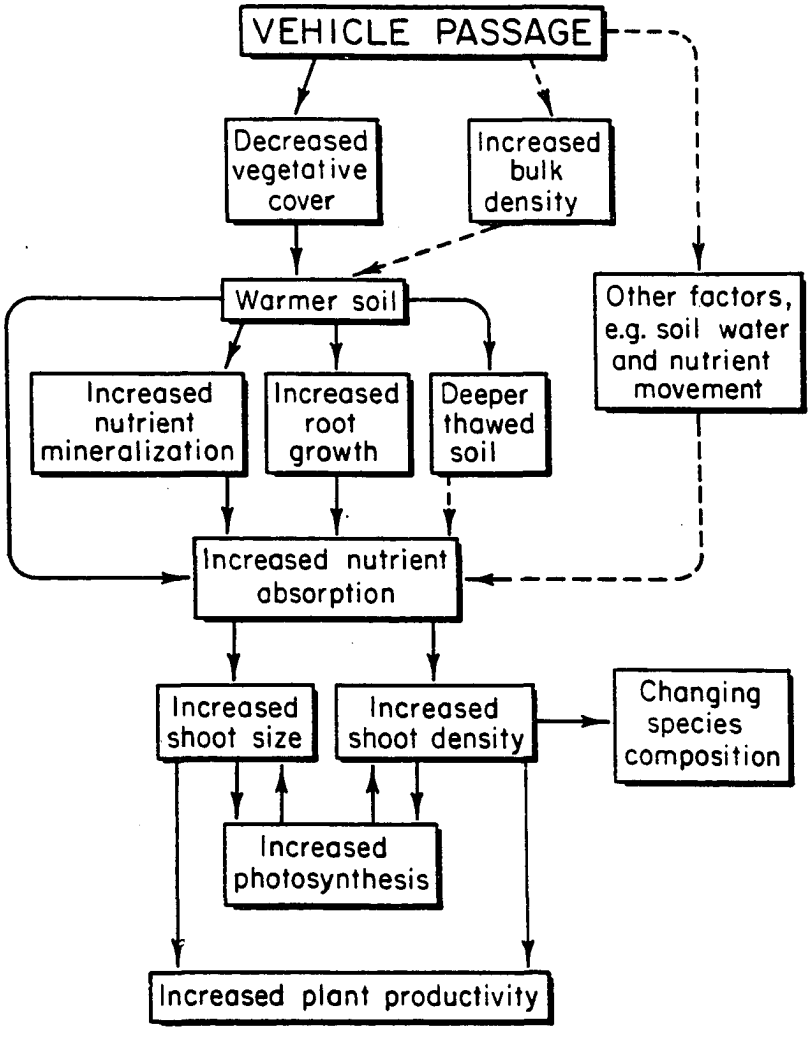

FIG. 1-2. Diagrammatic representation of causal relationships among factors linking vehicle passage in tundra to increased plant productivity. Broken arrows indicate suggested effects. (From Chapin & Shaver 1981).

tundra, thermokarst processes have led to the development of areas of standing water. These areas have become dominated by Eriophorum angustifolium and Carex aquatilis, species characteristic of wet meadow tundra and pond margins (Chapin & Shaver 1981).

In predicting the effects of this type of disturbance, it is important to recognize that, at least on the ecological time scale, there can be more than one endpoint of succession in a region. If a disturbance has drastically altered physical conditions, revegetation alone will not restore the original community. If this is desired, physical alterations (to drainage etc.) may be effective in some cases. Where the conditions have been greatly changed, it may not be feasible to return the site to a condition that will allow the growth of the original vegetation. Then, it will be instructive to study natural habitats which resemble the modified site, in order to determine what kind of successional processes and communities are possible.

RESTORATION OF XERIC DISTURBED SITES

Xeric sites such as roads, drill pads, camp pads and gravel pits have minimal development of organic soil and very few buried seeds or other propagules (Cargill unpubl.). Recovery of these sites represents a primary successional process which may resemble primary succession after natural disturbance on glacial till (Crocker & Major 1955; Viereck 1966) and riparian gravels (Bliss & Cantlon 1957; Robus 1981; Moore 1983).

Colonization of xeric disturbed sites is almost completely dependent on current seed rain. However, the dominant species of the surrounding mesic or wet tundra, which have the best opportunity to disperse onto the sites, are poorly adapted for growth in xeric conditions. Successful colonizers are more likely to be species from naturally-occurring gravelly sites, a habitat type of limited extent. Although the total seed rain onto xeric sites may be large, dispersal of species able to survive on the sites may be limiting. If this is the case, sowing or planting of appropriate native species may greatly speed recovery.

Provision of favorable microsites for germination may also be critical, even on sites with adequate natural seed rain. The coarse soil texture and lack of organic

matter on many xeric sites cause rapid moisture loss from the surface layer. Conditions for germination are improved around larger stones which shade the soil surface and reduce evaporation. High levels of NPK fertilizer, as often used in revegetation, can inhibit germination of Salix alaxensis (Chapter 3).

Because of the harsh abiotic conditions on xeric disturbed sites, pioneer species may facilitate colonization by later-successional species. In several natural systems with similar conditions, species with symbiotic nitrogen fixation (Dryas drummondii, Alnus and legumes) are important colonizers (Robus 1981) and presumably increase the availability of nitrogen for other plants. On some British mine spoils, sowing legumes has been effective in promoting the establishment of other species (Dancer et al. 1977; Palaniappan et al. 1979; Marrs et al. 1980; Jefferies et al. 1981; Roberts et al. 1981). Native legumes are important colonizers on arctic riparian gravels and some disturbed sites, and may prove useful for restoration.

Non-symbiotic species may also have facilitative effects, mainly because accumulation of organic matter increases the cation exchange capacity and moisture retention of the soil. Following glacial recession at Glacier Bay, Alaska, early colonization by willow and

alder appear to be equally beneficial for the establishment of spruce seedlings (Cooper 1923). By analogy, surface treatments to increase moisture retention or organic content may facilitate colonization and establishment of a community of native species. However, sowing of non-native grasses apparently inhibited invasion of abandoned gravel pads by native plants in arctic Alaska, despite poor survival of the grasses (Johnson & Van Cleve 1976; Neiland et al. 1981). The grasses grew rapidly in the first one or two seasons, and may have tied up much of the available nutrient pool. Germination and seedling establiishment may also be inhibited by the large quantities of litter and standing dead grass.

CONCLUSIONS

In order to select appropriate restoration methods for disturbed sites in tundra, some understanding is needed of the successional processes likely to be operating. Without such knowledge, the results of restoration attempts are unpredictable. Different combinations of successional mechanisms can be expected in different types of tundra sites. Successional trends will also differ according to whether only native species are involved, or introduced species also. In general, it will

be much more difficult to predict the effects of interactions involving non-native species.

Facilitative interactions among species are more likely to occur on sites where the initial conditions are very harsh (lack of moisture, low nutrients, etc.). Facilitation is more likely between native plants than when exotic species are involved, because the introduced species are likely to be fast-growing and highly competitive.

On mesic sites where the initial conditions are fairly favorable for at least some native species, early colonizers are more likely to inhibit later arrivals than to facilitate their establishment. This effect is likely to be increased if the early colonizers are non-native grasses which accumulate nutrients very effectively.

ACKNOWLEDGMENTS

Research leading to these generalizations was funded by the U.S. Army Research Office and the National Science Foundation (DPP-8602568) in grants to the University of Alaska.

CHAPTER 2

PATTERNS OF NATURAL REVEGETATION ON ABANDONED GRAVEL PADS IN ARCTIC ALASKA[1]

SUMMARY

(1) Abandoned gravel pads were colonized mainly by plant species whose natural habitat is riparian gravel bars.

(2) Eight years after abandonment, mean total cover of native vascular plants was 2.7%, and mean number of species per site was 4.4. Five of the nine most frequent colonizing species were riparian legumes. There were no successful colonizers from adjacent moist and wet tundra communities.

(3) Distance from seed sources in the riparian zone explained 25% of the variance in cover of native species and 40% of the variance in number of species per site. The distribution of legumes was more restricted to sites near the Sagavanirktok River than was the distribution of non-legumes.

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[1]Susan M. Cargill and F. S. Chapin, III. Submitted to The Journal of Applied Ecology.

(4) Soil pH, content of organic matter and fine particles, latitude and cover of non-native grasses did not contribute significantly to explaining variation among gravel pads in cover, diversity and distribution of native plants.

(5) We attribute the low cover and diversity of native plants on abandoned gravel pads to a combination of dispersal limitation, lack of water for germination and slow growth due to limited availability of mineral nutrients.

INTRODUCTION

To prevent melting of permafrost, camps, work sites and roads in arctic regions are often constructed on gravel pads up to 1.8 m thick. Most gravel pads along the arctic section of the Trans-Alaska Pipeline were fertilized and seeded with non-native grasses, but these revegetation attempts have been largely unsuccessful (Van Cleve & Manthei 1972; Johnson 1981). Revegetation with exotic species has also met with limited success on other types of arctic disturbed sites (Younkin 1976; Van Cleve 1977; Johnson 1981).

Sowing of non-native grasses on gravel pads was expected to facilitate the colonization of the sites by native species, by ameliorating the physical environment (Lucas 1975). However, the available data suggest that fertilizing and seeding may inhibit natural revegetation (Johnson 1981; Neiland et al. 1981; Walker et al. 1987).

Recently, considerable interest has developed in alternative approaches to restoration, including direct seeding and planting of native species (Neiland et al. 1981), fertilizing adjacent tundra to increase seed production of native plants (Chapin & Chapin 1980), or leaving disturbed sites alone to revegetate naturally. Better understanding of natural colonization and succession processes in the Arctic is needed if restoration methods for gravel pads and other disturbed sites are to be improved (Johnson & Van Cleve 1976; Gartner, Shaver & Chapin 1983; Walker et al. 1987).

Possible limitations to the invasion of gravel pads by native plants include dispersal of propagules, limited availability of moisture and nutrients due to the physical properties of the substrate, and competition or interference from the non-native grasses. The physical characteristics of riparian gravel bars resemble those of gravel pads, so riparian species may be more likely than others to successfully colonize gravel pads. Arctic

riparian areas are subject to frequent natural disturbance, and their flora includes a high proportion of pioneer species (Drury 1956; Bliss & Cantlon 1957; Viereck 1970, Johnson & Van Cleve 1976). However, dispersal limitations could restrict establishment of riparian species on sites distant from seed sources.

The objective of this study was to determine which environmental factors were important in explaining the variation in natural revegetation among 16 abandoned gravel pads in arctic Alaska.

METHODS AND MATERIALS

Study area

The study sites were on the North Slope of Alaska, i.e., the area between the crest of the Brooks Range and the Arctic coast. All sites were adjacent to the Dalton Highway, which runs NNE from the Brooks Range to Prudhoe Bay at the coast. Distances of sites from the Sagavanirktok River ranged from 0.1 to 15 km. The southernmost site (Site 1) was at Toolik Lake ($68^{o}40'$ N, $149^{o}40'$ W), 206 km on the road from Prudhoe Bay. The northernmost site (Site 16) was near Franklin Bluffs

(69°45' N, 149°,20' W), 56 km from Prudhoe Bay. Sites 15 and 16 were on the arctic coastal plain, and all the other sites were in the rolling northern foothills of the Brooks Range. Details on location of all sites are given in Appendix 1. The sites were abandoned approximately 10 years prior to the study (i.e., about 1976), and most were fertilized and seeded with non-native grasses 1 or 2 years after abandonment (Johnson 1981). All the study sites were raised gravel structures, originally used either as camp sites or roads. The pads are constructed of coarse gravel, with little organic matter or fine material present, so water holding capacity and nutrient availability are low. Particles < 2 mm in diameter are virtually absent from the surface layer.

The gravel pads resemble riparian gravel bars on the North Slope, which are periodically droughty, light textured, lacking a surface organic layer and of moderate nutrient status (Bliss & Cantlon 1957). The availability of nutrients, particularly N and P, is low in alluvium of the Sagavanirktok River and other rivers originating in the limestone mountains of the central Brooks Range (Neiland et al. 1981). Some of the gravel bars lack fine particles in the upper horizons, possibly due to a winnowing effect of water movement or other sorting processes (Leopold, Wolman & Miller 1964).

Annual precipitation in the foothills is 10-20 cm, most of which falls as rain during the summer (Spetzman 1959). The summer thaw period lasts about 90 days (Walker et al. 1987), but freezing temperatures and snow may occur in any month. Warm dry weather (25°C or higher) is fairly common in June and July. Winter snow accumulations are modest, particularly in areas exposed to winter winds. The physiography and climate of the area are described in more detail by Moore (1983) and Walker et al. (1987).

Soil characteristics

Ten soil samples were collected from each site. Sample size was 10 for all soil analyses except particle size, for which 5 samples from each site were used. Content of stones was determined by passing the samples through a 2 mm sieve and weighing the two fractions. The material with particle size < 2 mm was subjected to mechanical analysis (Bouyoucos hygrometer method, Gee & Bauder 1986) to determine the proportions of sand, silt and clay. Water content was determined gravimetrically by comparing fresh weight with weight after oven drying at 60°C to constant weight. Samples were oven dried and weighed before sieving, and the weight of stones subtracted from both fresh and dry weights. This prevented

errors due to water loss during sieving. Soil pH was estimated for samples diluted 10:1 in 0.1 M CaCl, using a pH meter with a glass electrode. Organic matter content was estimated by weight loss on ignition of the sieved (< 2 mm) soil (Jackson 1958). Samples were weighed before and after being placed in a muffle furnace for 7 h at 400°C.

Transects

Vegetation cover was estimated using a point-intercept method. Because the total cover was very low, it was necessary to sample a large area in order to accurately estimate cover (Mueller-Dombois & Ellenberg 1974), so sample points were spaced widely.

Twenty transects were laid out at each site, spaced equally along the long axis of the site. Lengths of transects varied among sites (10 - 20 m), but all transects within a site were approximately the same length. Cover was assessed at a single point every 0.5 m along the transect. The points were located using a wooden frame (25 x 25 cm) with clear monofilament crosshairs strung above and below the frame. Thus, when the frame was laid next to the measuring tape, a single point, aproximately 12.5 cm from the tape, was objectively

defined. All sampling was done between June 19 and July 11, 1986. To eliminate bias due to changes in cover through the season, sampling dates were chosen so as not to vary systematically with either distance from the river or latitude.

Most plants were readily identifiable to species, the only important exceptions being small willow (Salix) seedlings. Seedlings of S. alaxensis were easiliy distinguishable, but other species could not be identified definitively. These unidentified seedlings have been grouped as Salix spp., but most are probably S. glauca. Plant nomenclature follows Hulten (1968). Non-native grasses were not identified to species, but live and dead grass were recorded separately.

The number of sampling points per site varied slightly but averaged approximately 1000. Data for each site were adjusted by dividing the number of species observed by the number of sampling points and multiplying by 1000, to facilitate comparisons. Only species which occurred on the transects were included.

Dispersal of willow seeds

Dispersal of seeds from riparian willow stands (mainly S. alaxensis) was examined at 2 sites (#8 and #9) where such stands were present. Seed traps (plastic trays, 50 cm x 50 cm x 5 cm) were placed at intervals of a few meters along a transect perpendicular to the river bank. Total lengths of the transects were approximately 50 m and 200 m at sites 8 and 9 respectively. The trays were filled approximately 2/3 full of water, and replenished twice weekly to ensure they were never empty. At each visit, any willow seeds present were removed and counted. The seed traps remained in place from July 2 to July 12, 1986, which encompassed most of the period of willow seed dispersal.

Statistical Analysis

Detrended correspondence anaylsis (DECORANA, Cornell Ecology Programs) was used to summarize the species-by-samples data matrix, with each site considered one sample. This ordination procedure, based on reciprocal averaging, finds new axes which best explain the variation in both distribution patterns of species and species composition of samples (Gauch 1982). The final score for a species is

an average of the scores for the samples in which it occurs, while the score for a site is the average of the scores for the species it contains.

Stepwise multiple linear regression (BMDP 2R) was used to determine which of the independent variables (distance from river, distance south from the arctic coast, grass cover, soil texture, pH and organic matter) were important in explaining variation in the dependent variables (number of native species per site, total cover of native species, and site scores on the first DECORANA axis). In this procedure, the independent variable which explains the largest portion of the variation in the dependent variable is entered into the model at the first step. At the second step, the variable which contributes most to explaining the remaining variation is entered, and so on. To eliminate problems with multicollinearity, this program screens out independent variables which are highly correlated with other independent variables already included in the model. The analyses reported here were based on the ranks of the observations for all variables, rather than on the actual data. This transformation makes the analysis less sensitive to outliers and non-normality than is the usual procedure (Conover 1980).

RESULTS

Soil characteristics

Soils of the gravel pads contained 30 - 63% by dry weight gravel (particles > 2 mm in diameter). Of the material < 2mm in diameter, 77-92% was sand, so the soils could all be classified as sands or loamy sands (Brady 1974). Organic matter content was between 1% and 3% at all sites but one, which had 5% organic matter. These values are low to moderate for mineral soils. Soil pH was neutral to slightly alkaline (7 to 8). Water content (of the fraction < 2 mm in diameter) ranged from 2 to 15%. Data on soil characteristics for individual sites are given in Appendix 1.

Species composition

Nineteen species of native plants were observed on the transects at the 16 study sites. Of these, 9 species, including 5 legumes, and the *Salix* spp. group, occurred on 4 or more sites, and were considered important pioneer taxa (Table 2-1). Complete data on species composition of each of the 16 sites are given in Appendix 1. These species all occur naturally on riparian gravel bars, and some (e.g., *Oxytropis borealis*, *Equisetum arvense*) are

TABLE 2-1. Frequencies (number of sites where the species occurred) and mean cover values (over all sites) of all native vascular plant species observed on transects on 16 abandoned gravel pads. First axis DECORANA scores are given for species which occurred on 4 or more sites.

Species	Frequency	Cover (%)	DECORANA score
Equisetum arvense (Equisetaceae)	11	1.2	74
Oxytropis borealis (Leguminosae)	9	0.3	-9
Salix spp. (glauca) (Salicaceae)	8	0.2	185
Astragalus alpinus (Leguminosae)	5	0.3	-3
Hedysarum mackenzii (Leguminosae)	5	0.1	-22
Epilobium latifolium (Onagraceae)	4	0.2	337
Hedysarum alpinum (Leguminosae)	4	<0.1	-13
Oxytropis campestris (Leguminosae)	4	0.2	34
Salix alaxensis (Salicaceae)	4	0.1	165
Dryas integrifolia (Rosaceae)	3	0.1	
Astragalus aboriginum (Leguminosae)	2	0.1	
Astragalus eucosmus (Leguminosae)	2	0.1	
Crepis nana (Compositae)	2	<0.1	
Lupinus arcticus (Leguminosae)	2	<0.1	
Carex bigelowii (Cyperaceae)	1	<0.1	
Epilobium angustifolium (Onagraceae)	1	<0.1	
Minuartia biflora (Caryophyllaceae)	1	<0.1	
Oxytropis nigrescens (Leguminosae)	1	<0.1	
Shepherdia canadensis (Eleagnaceae)	1	<0.1	

also common in upland tundra on old floodplain terraces. None is important in the wet or moist sedge tundra which are the dominant vegetation types adjacent to the gravel pads. The number of species observed on a single site (adjusted to 1000 sample points) varied between 0 and 11.1, with a mean of 4.4 (Table 2-2).

In the stepwise regression analysis, distance from the river was the only independent variable entered into the model and explained 40% of the variance in number of native species ($p < 0.05$, Table 2-3). The negative regression coefficient indicated that sites nearer to the river had more species per 1000 sample points than did sites further from the river (Fig. 2-1). The stepwise procedure stopped at this point because none of the other independent variables explained a significant proportion of the remaining variance in number of native species.

Cover of native species and sown grass

The total cover of native species on the disturbed sites ranged from 0 to 8.6%, with a mean of 2.7% (Table 2-2). On the 14 sites which had been seeded with non-native grasses, total grass cover ranged from 26% to 70%, with a mean of 40%. The mean cover of live grass was approximately 7%.

TABLE 2-2. Location and vegetation data and first axis DECORANA scores for 16 abandoned gravel pads in arctic Alaska. No DECORANA score could be calculated for site 5 because it was devoid of native plants.

	Distance from		Native species		Sown grass cover (%)		
Site	Sag River	Prudhoe Bay	No. spp.	Cover (%)	Total	Live	1st axis DECORANA score
1	12.0	206	4.9	3.6	7	3	303
2	15.0	200	0.8	1.1	45	11	79
3	8.0	189	0.0	0.0	53	7	101
4	5.5	187	1.2	0.4	64	9	101
5	5.0	181	0.0	0.0	26	8	
6	4.0	179	2.7	0.4	70	15	104
7	0.1	165	11.1	4.3	54	9	72
8	0.1	163	4.6	8.3	58	6	61
9	0.1	163	9.7	2.4	34	5	84
10	0.2	160	6.4	2.8	37	9	79
11	0.1	142	5.6	8.6	27	4	70
12	0.2	128	3.3	1.0	55	8	85
13	0.5	126	9.0	7.5	0	0	113
14	0.2	126	2.9	1.4	0	0	146
15	0.2	58	3.0	1.4	34	16	0
16	0.1	56	4.4	0.5	8	6	13
Mean			4.4	2.7	40	7	

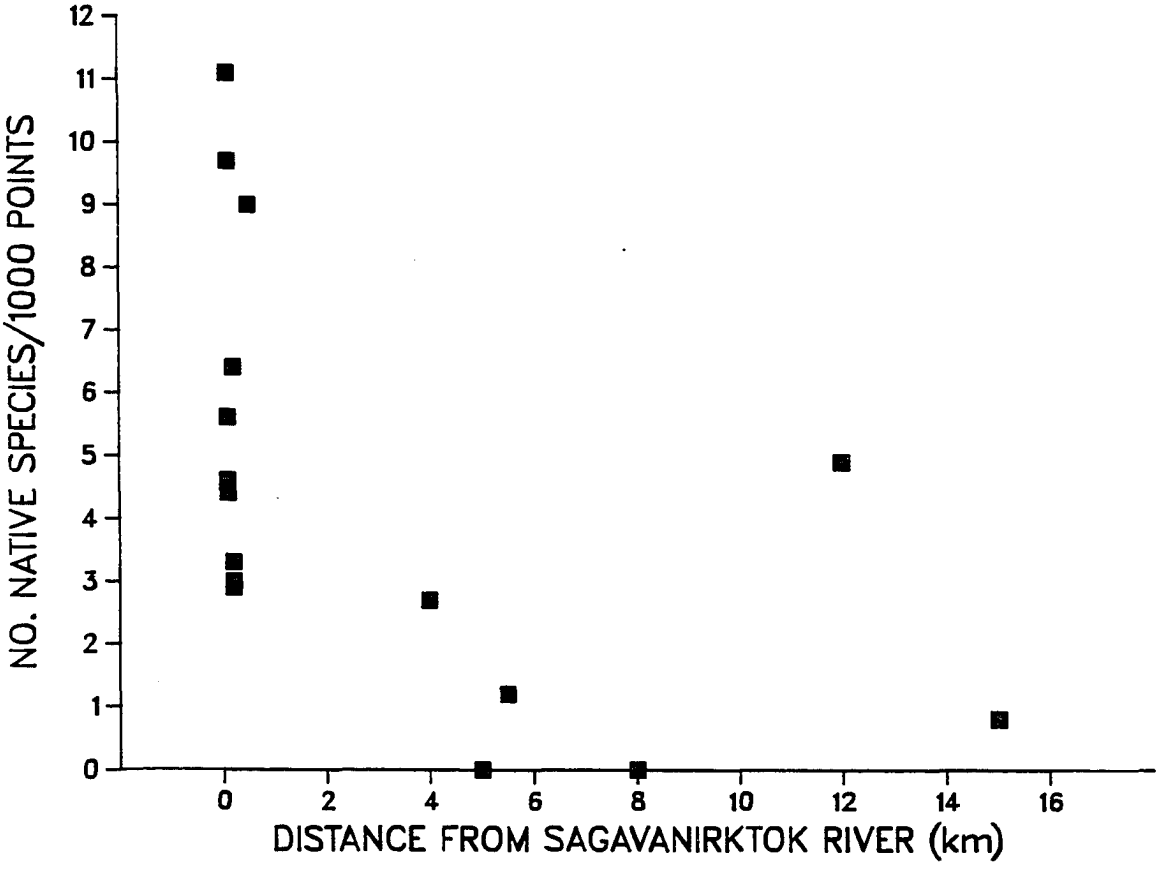

FIG. 2-1. Scatter plot of number of native species vs. distance from Sagavanirktok River for 16 abandoned gravel pads. Regression coefficient = -0.64 ($P < 0.05$).

Distance from the Sagavanirktok River was the only independent variable to enter the stepwise regression model and accounted for 25% of the variance among sites in total cover of native species ($P < 0.05$, Table 2-3). The regression coefficient was negative, meaning that cover was higher on sites nearer the river (Fig. 2-2). None of the other independent variables contributed significantly to explaining the remaining variance in cover of native species.

DECORANA ordination

The eigenvalue of 0.68 for the first DECORANA axis is roughly equivalent to the proportion of variance explained (Gauch 1982). Species scores on the first axis separated the legume species (low scores) from the non-legume species (high scores), indicating that the two groups have different distribution patterns (Table 2-1). Epilobium latifolium scored more than 100 points higher than any other species, reflecting a unique distribution. Site scores were therefore lower for sites dominated by legumes and higher for those colonized mainly by willows and/or E. latifolium.

The only independent variable entered into the stepwise regression model was distance from the

TABLE 2-3. Results of stepwise multiple linear regression on ranks, with number of native species, total cover of native species or first axis DECORANA score as the dependent variable. In each case, distance from the Sagavanirktok River was the only independent variable which explained a significant ($P < 0.05$) amount of the variance in the dependent variables.

Dependent variable	Regression coefficient	% variance explained
No. of native spp.	-0.64	40
Total native cover	-0.51	25
DECORANA score	0.56	30

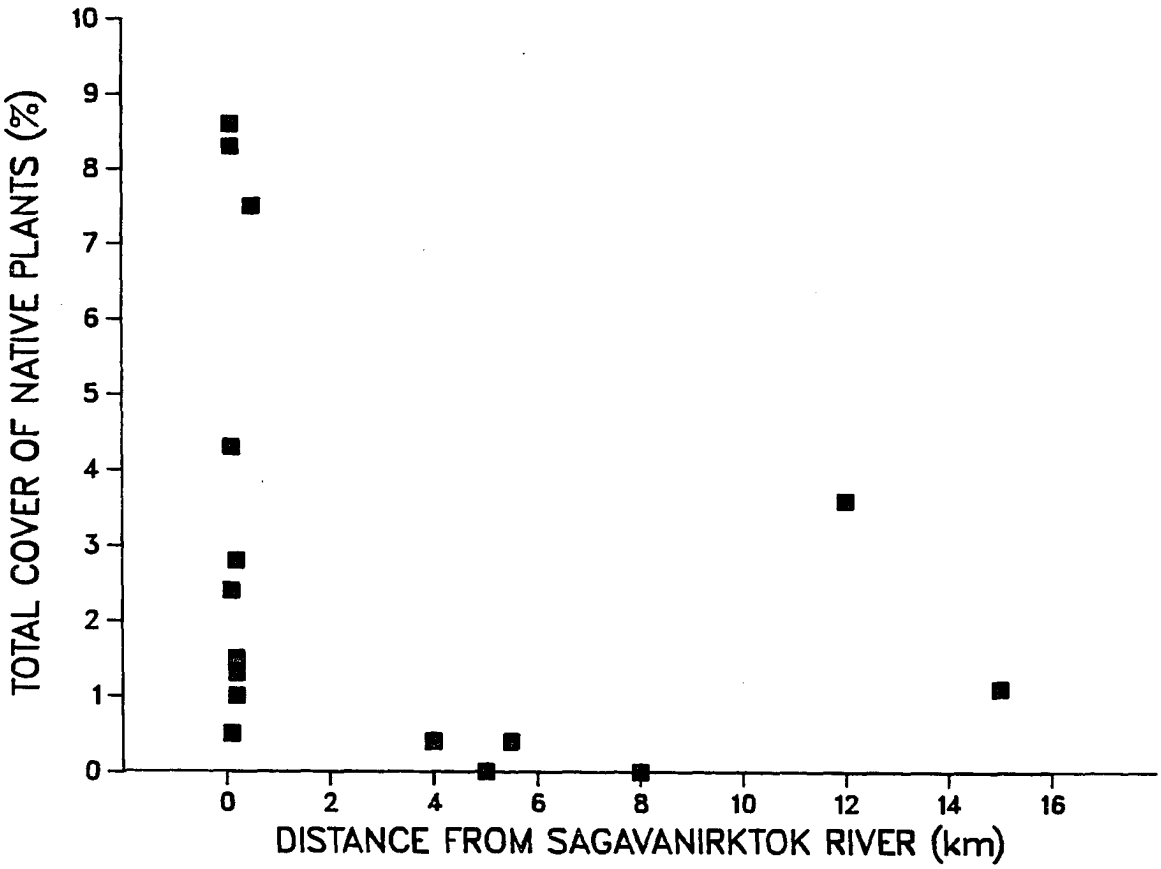

FIG. 2-2. Scatter plot of total cover of native species vs. distance from Sagavanirktok River for 16 abandoned gravel pads. Regression coefficient = -0.51 ($P < 0.05$).

Sagavanirktok River, which explained 30% of the variance in first axis DECORANA scores ($P < 0.05$, Table 2-3). The regression coefficient was positive, indicating that sites near the river had a higher proportion of legumes among the colonizers while sites further from the river had relatively more willows and E. latifolium (Fig. 2-3). This resulted mainly from the points for sites 1, 15 and 16. Site 1 was 12 km from the river and had a first axis score of 303, reflecting a high cover of E. latifolium. Sites 15 and 16 were adjacent to the river and had first axis scores of 0 and 13 respectively, reflecting complete absence of non-legumes. None of the other independent variables contributed significantly to explaining the remaining variance in first axis scores.

Dispersal of willow seeds

The number of seeds of S. alaxensis falling into seed traps declined significantly with distance from riparian willow thickets (Fig. 2-4). High numbers of seeds (>5 per m^2) were only observed in traps < 20 m from the seed sources.

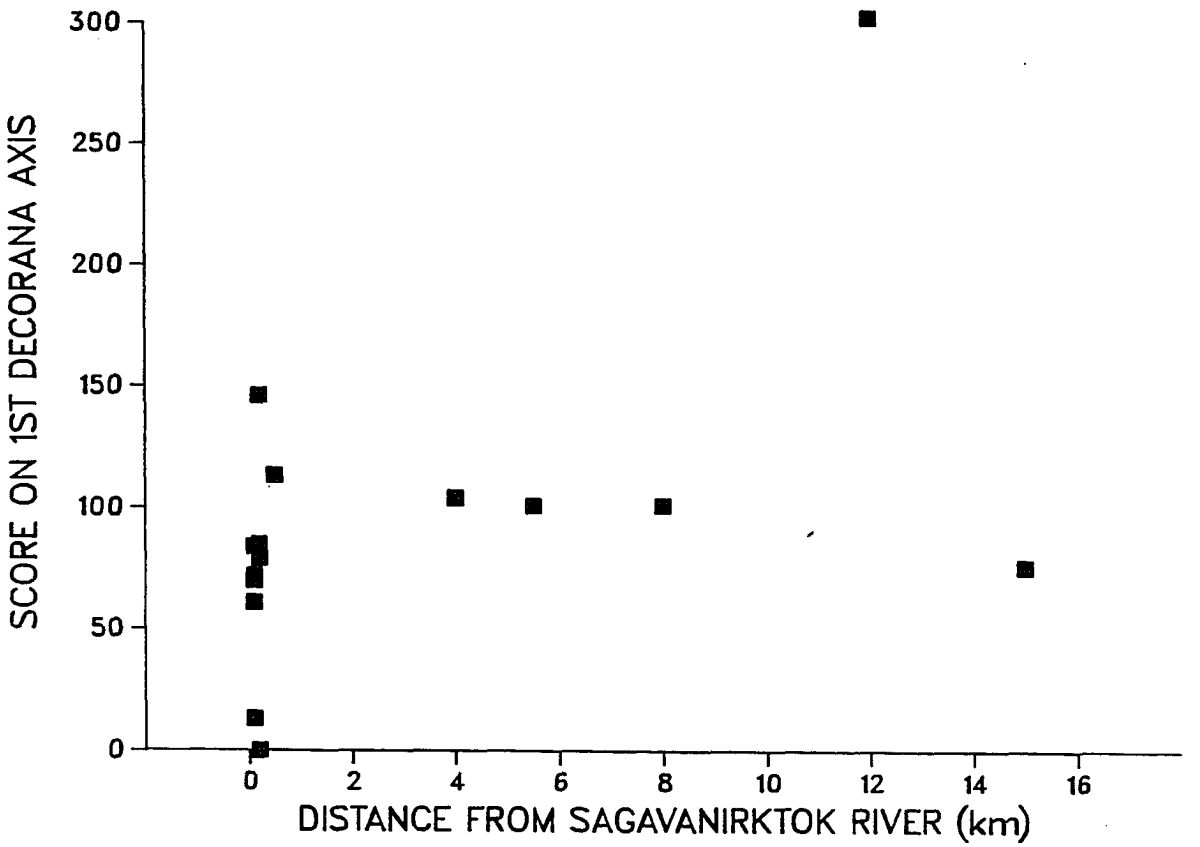

FIG. 2-3. Scatter plot of scores on 1st DECORANA axis vs. distance from Sagavanirktok River for 16 abandoned gravel pads. Regression coefficient = 0.56 ($P < 0.05$).

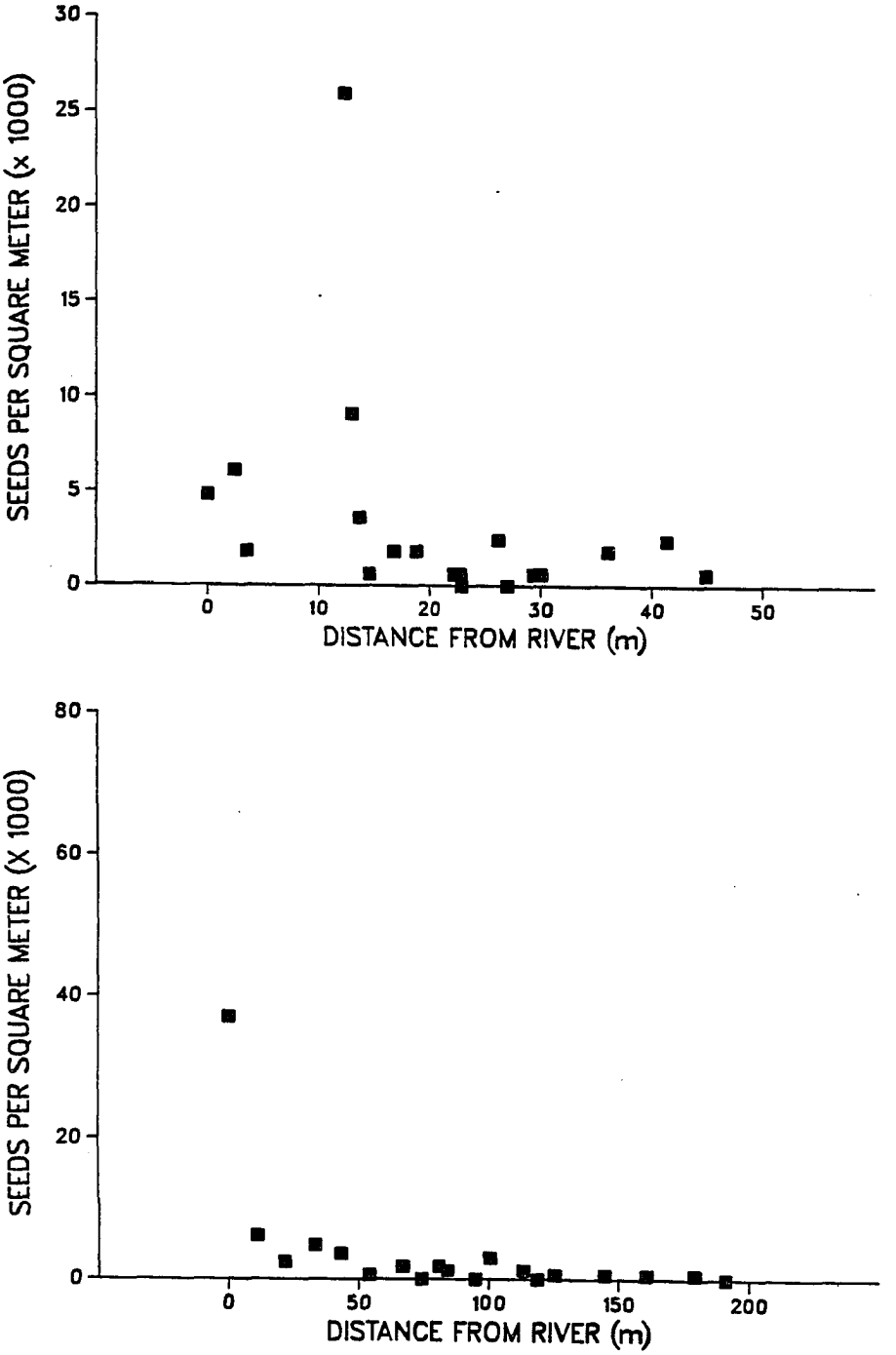

FIG. 2-4. Numbers of willow seeds per m^2 in seed traps placed at varying distances from riparian willow stands at sites 8 and 9. Spearman's rank correlation = -0.57 ($P < 0.01$) for site 8 and -0.71 ($P < 0.001$) for site 9.

DISCUSSION

The cover and diversity of native plants on abandoned gravel pads were low overall and varied among the 16 sites studied. The research reported here focused on explaining the variability among the sites.

Distance from riparian seed sources explained 25% of the variance among sites in cover of native species and 40% of the variance in number of species per site, reflecting the dominance of the pioneer community by species adapted to riparian gravel bars. Salix alaxensis, Epilobium latifolium and several of the legumes found on gravel pads are characteristic of successional communities along the Colville River in arctic Alaska (Bliss & Cantlon 1957). Gill (1972) noted Hedysarum alpinum among pioneer species in riparian communities of the Mackenzie River in the Northwest Territories of Canada. Some 10-year-old gravel pads in the Prudhoe Bay area developed a sparse cover of mainly riparian species (Walker et al. 1987). In contrast, riparian pioneer species were mostly lacking from 25-year-old gravel runways in the Cape Thompson region, Alaska (Everett et al. 1985).

The lack of strong correlations of cover and diversity with soil variables (pH, organic matter, texture) may simply reflect the similarity of these

characteristics for most gravel pads. Soil pH of all sites but one was between 7 and 8, a range within which the availability of major nutrients varies little (Brady 1974). Organic matter content, which affects availability of both water and nutrients, was moderate (1-3%) at most sites. Soils were gravelly at all sites, and the percentage of silt and clay in the < 2mm fraction was uniformly low (< 25%), indicating low water holding capacity at all sites.

Availability of seed was also more important than soil factors in determining the degree of colonization of a disturbed site in tussock tundra (Gartner, Shaver & Chapin 1983), but in this case recruitment was mainly from the buried seed pool.

The DECORANA ordination revealed different distribution patterns for legumes and non-legumes. Stepwise regression on the first axis scores indicated that legumes were more restricted to sites near the river than were non-legumes, reflecting differences in dispersal capabilities. The legumes have relatively heavy seeds with no adaptations for wind dispersal, and are probably normally dispersed by water movement, or blown over the surface of the snow in winter (Savile 1972), while willows, fireweed and Equisetum all have light, wind-dispersed propagules.

Kubanis (1980) examined the vegetation of a large number of disturbed sites along the Trans-Alaska Pipeline, including some in the arctic portion, in 1978 and 1979. There was remarkably little similarity between the species she observed then, and those recorded in our study. Unfortunately, she did not present data for individual sites, so direct comparisons cannot be made. Kubanis recorded 13 species of exotic weeds on sites north of the Brooks Range, but these have now almost disappeared and were never encountered on any of the study sites. Epilobium latifolium, Equisetum arvense and Salix spp. (presumably including S. alaxensis) were among the native species she observed, but legumes were virtually absent. Slower colonization by legumes may be at least partly attributable to their larger seed size.

The total cover of grass (live + dead) on the sites averaged 40%, but the average cover of live grass was only 7%. This contradicts Hubbard's (1980) claim that all lands disturbed by construction had been successfully restored by January of that year. Kubanis (1980) reported that grass cover on disturbed sites along TAPS declined in the first 3 years of sowing, and that the average cover never exceeded 20%. Chapin & Chapin (1980) found that exotic grasses planted in an alpine area in interior Alaska were almost completely eliminated after 5 years.

There was no indication that the sown grass facilitated invasion by native species. Cover of sown grass did not contribute significantly to explaining either cover or diversity of native plants. Possible negative effects of grass on invasion by native plants include competition for water and nutrients, mechanical interference with wind-borne seeds reaching suitable germination sites, and inhibition of nitrifying bacteria (Rice & Pancholy 1972). At Chena River Lakes, in interior Alaska, sown grass decreased the growth of transplanted willow seedlings (Johnson, Rindge & Gaskin 1981). Chapin & Chapin (1980) found no consistent effect of exotic grasses on the establishment of native sedges (Eriophorum vaginatum and Carex bigelowi). On arctic disturbed sites along TAPS, numbers of naturally occurring willow seedlings were negatively related to the cover of sown grass (Neiland et al. 1981).

The preponderance of legumes among the pioneer taxa of gravel pads is striking, and suggests that nitrogen supply is an important factor limiting plant growth on these sites. Legumes and other plants with symbiotic nitrogen fixation are also important in primary succession on some northern floodplains (Bliss & Cantlon 1957; Gill 1972; Walker & Chapin 1986), glacial outwash (Viereck 1966), and gravel exposed by retreating glaciers (Lawrence

et al. 1967). Legumes have been planted successfully on disturbed soils severely lacking in organic matter; in addition to providing cover, they increased the soil nitrogen available to other plants (Palaniappan, Marrs & Bradshaw 1979; Jefferies, Bradshaw & Putwain 1981; Jefferies, Willson & Bradshaw 1981).

Plants adapted to riparian gravel bars are apparently better able than other species to colonize gravel pads, but the degree of invasion is limited by distance from seed sources in the riparian zone. Lack of moisture for germination (Chapters 3, 4) and lack of nutrients for growth (Chapter 3) also limit the extent of natural revegetation. Variation among sites in the extent of colonization is due more to limitations of dispersal than to the unfavorable substrate conditions. Sowing or planting of riparian legumes may be a useful approach to restoration of gravel pads; they grow well on such sites when they are present.

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CHAPTER 3

ESTABLISHMENT OF *Salix alaxensis* ON ABANDONED GRAVEL PADS IN ARCTIC ALASKA[1]

SUMMARY

(1) The purpose of the study was to examine the effects of water and nutrient availability on germination, survival and growth of *Salix alaxensis* on abandoned gravel construction sites (pads) in arctic Alaska.

(2) Germination of *S. alaxensis* on abandoned gravel pads was strongly limited by moisture. In field plots, watering or addition of stones to the surface enhanced germination. In pots, the addition of fertilizer reduced germination. Seeds failed to germinate at water potentials below -0.2 MPa.

(3) The availability of water and nutrients on gravel pads did not limit the survival of established seedlings of *S. alaxensis*.

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(4) The addition of NPK fertilizer significantly increased growth of seedlings that were watered during the establishment period, but seedlings that were not watered showed no response to nutrient addition. After the initial establishment period, water availability did not limit seedling growth.

(5) Transplanting S. alaxensis seedlings onto abandoned gravel pads would be practical where shrubs are required to replace lost wildlife habitat or for esthetic reasons.

INTRODUCTION

During construction of the arctic portion of the Trans Alaska Pipeline System (TAPS), roads, worksites and camps were all placed on raised gravel structures (pads) to prevent thermal erosion of the underlying permafrost. Most of the gravel was mined from the floodplains of the Atigun and Sagavanirktok rivers. The pipeline right of way, camps, workpads and roads were also located within the floodplains. This resulted in the destruction of riparian shrub communities, which are important to wildlife, including caribou Rangifer tarandus (White and Trudell 1980), muskox Ovibos moschatus (Robus 1981) and moose Alces alces (Mould 1977). Of particular concern was

the destruction of over 80 ha of thickets dominated by Salix alaxensis (Anderss.) Cov., the primary winter browse species for moose (Mould 1977).

Because of the importance of riparian willows to moose and other wildlife, several attempts have been made to plant seedlings or cuttings on abandoned workpads and other disturbed sites, with mixed results (Neiland et al. 1981). Willows were established successfully on some sites both within and outside the active floodplains of the Sagavanirktok and Atigun rivers. However, the factors that prevented establishment on other sites were unclear. The substrate was similar for all sites, since gravel pads outside the floodplains were constructed with materials from the floodplains. Natural regeneration of willows occurred on some sites, but this often involved species less palatable to moose than S. alaxensis.

We hypothesized that both natural establishment of S. alaxensis on abandoned gravel pads and the success of plantings are limited by the availability of water and mineral nutrients. We examined the effects of these factors at two critical stages of the life cycle:
1. Germination 2. Seedling growth and survival.

METHODS AND MATERIALS

Study area

Transplant gardens were established at four sites on the North Slope of Alaska, i.e., the area north of the crest of the Brooks Range. The main garden was on the site of an abandoned pipeline construction camp adjacent to Toolik Lake, in the northern foothills of the Brooks Range ($68^{o}40'N$, $149^{o}40'W$). Two other sites, both abandoned access roads to gravel pits, were also within the foothills province, at Material Site (MS) 118 ($68^{o}41'$ N, $149^{o}08'W$) and Material Site (MS) 120 ($68^{o}52'$ N, $148^{o}49'W$). These sites are approximately 20 km and 43 km, respectively, N of Toolik Lake. The northernmost site, Franklin Bluffs ($69^{o}44'N$, $149^{o}20'W$), is an abandoned camp pad on the arctic coastal plain, approximately 150 km N of Toolik Lake. All sites except Toolik are within the inactive floodplain of the Sagavanirktok (Sag) River.

Availability of nutrients, particularly N and P, is low in natural gravel bars on the Sag river due to low organic content, low cation exchange capacity and high pH (Neiland et al. 1981; Chapter 2). The high pH is due to the origin of the river in a limestone-rich area of the Brooks Range. Some of the gravel bars lack fine particles

in the upper horizons, due to a winnowing effect of water movement or or sorting processes which leave the larger particles on the surface (Leopold et al. 1964, Everett et al. 1985). The lack of fine particles results in low water holding capacity and cation exchange capacity.

Annual precipitation in the foothills is 10-20 cm, most of which falls as rain during the summer (Spetzman 1959). Despite low annual precipitation, low rates of evapo-transpiration in the Arctic generally allow for net accumulation of moisture during the growing season (Britton 1966). Freezing temperatures and snow may occur at any time, but warm days (25^{o}C or higher) are common during June and July. Winter snow accumulations are modest, particularly in areas exposed to winter winds. Drifts in low-lying and sheltered areas provide protection from wind and blowing snow in winter, and additional water in spring, but may shorten the growing season.

Germination

Catkins were collected from approximately 20 individuals in the Toolik Lake area at the time of dispersal in July 1985. Seeds were removed from the catkins and pappus using compressed air and a stack of

soil sieves. In the field experiments, seeds were sown within 48 hours of collection.

The effects of osmotic potential on germination were examined in the laboratory using solutions of polyethylene glycol. Seeds were sown in Petri dishes (10 per dish), on filter paper moistened with polyethylene glycol solutions of 0, -0.1, -0.2, -0.5, -1.0, and -1.5 MPa. Required solution concentrations were calculated according to the formula:

$$Ys = -(1.18 \times 10^{-2})C - (1.18 \times 10^{-4})C^2 + (2.67 \times 10^{-4})CT + (8.39 \times 10^{-7})C^2T$$

where Ys = water potential of the solution (in bars), C = concentration of the solution (in g PEG kg^{-1} H_2O) and T = temperature (in ^{o}C). The dishes were weighed, placed in plastic bags and kept in a growth chamber at 20^{o}C in constant light. To maintain constant osmotic potential, dishes were weighed every 2 days, and distilled water was added to compensate for any weight lost. Germinated seeds were counted and removed every 2 days. The seeds used in this experiment had been frozen for 10 months. Final germination percentages were compared using Kruskal-Wallis tests (BMDP 3S) and multiple comparisons tests (Conover 1980).

The effects of water and fertilizer were examined by sowing fresh seed in 13 x 13 cm square pots of river sand, which were placed outdoors at Toolik Lake. Approximately 0.9 g of commercial NPK fertilizer (18% total N, 18% P_2O_5, 18% K_2O) was added to each fertilized pot at the time of sowing. This was equivalent to 555 kg ha^{-1}, slightly less than the amount of fertilizer added when non-native grass seed was sown on gravel pads by the pipeline construction company (Johnson 1981). Watered pots were watered whenever the soil became dry. A combined treatment and an untreated control were also included, making a 2x2 factorial design for water and nutrients. Ten seeds were sown in each pot, and ten pots were assigned to each treatment. Germination was checked daily, and germinated seeds were removed. The effects of fertilizer and water on final germination percentage were examined using 2-way analysis of variance (ANOVA, BMDP 2V).

Germination was also assessed in field plots. Five replicate blocks, each 1m x 1m, were laid out on the Toolik gravel pad. Each block was divided into 16 plots, 25 cm x 25 cm. Within each block, treatments (Table 3-1) were randomly assigned to alternate plots, so treated plots were separated by unused buffer plots. Approximately 200 seeds were sown by hand in each subplot. All subplots were watered at the time of sowing, but no additional

TABLE 3-1. Treatments applied to subplots to test effects on germination of *Salix alaxensis*.

Treatment	Description
Water	Watered whenever surface soil became dry, to increase availability of water.
Peat	Commercial *Sphagnum* mixed with surface layer (1-2 cm) of soil (approximately equal volumes of peat and soil), to improve water retention.
Sand	River sand mixed with surface layer of soil (approximately equal volumes of sand and soil), to reduce water retention by reducing % silt and clay sized particles.
Stones	Stones (up to 4 cm dia.) placed on the soil surface, covering approximately 75% of the area. This provided shaded, moister microsites.
Fertilized	Approximately 3.4g of fertilizer added to each subplot (equivalent to 555 kg/ha), to increase nutrient availabily and simulate conditions on sites seeded with non-native grasses.
Fert/Sand	Fertilizer and sand treatments combined.
Fert/Water	Fertilizer and water treatments combined.
Control	No treatments applied.

water was given except in the watered treatments. The fertilizer used was the same as that described above. Germination was checked after 5 days. Under ideal conditions in Petri dishes, germination was consistently > 90%, so the germination results are reported as percent of the total number of seeds sown. Final germination percentages for treatments were compared using Kruskal-Wallis tests (BMDP 3S) and multiple comparisons tests (Conover 1980).

Seedling transplants

The effects of water and fertilizer treatments were examined in a transplant garden on an abandoned gravel pad at Toolik Lake, using seedlings grown in the glasshouse from seeds collected in the study area. Smaller transplant gardens were set up at three other "non-intensive" sites, to examine the effects of fertilizer treatment and variation between sites.

Catkins of Salix alaxensis were collected near Toolik Lake at the time of seed dispersal (late June) in 1984. Seeds were separated from the catkins as described above, and stored frozen in sealed plastic containers for approximately 8 months.

The seedlings were grown at the Alaska State Forest Nursery at Eagle River, Alaska. The seeds were sown in a mixture of peat moss and vermiculite in individual plastic conetainers of approximately 20 cm^3, and recieved a single application of 20:20:20 fertilizer providing about 0.1 mg l^{-1} elemental N. In mid-July, when the seedlings were approximately 4 months old, they were transplanted to the field sites.

Because the gravel pads were compacted and rocky, each seedling was planted in a hole approximately 20 cm in diameter and 15 cm deep. A plug of the peat moss-vermiculite mixture remained attached to the roots of each seedling. At the main (Toolik) transplant site, seedlings were given 1 l water each at planting, and on 3 more occasions during the first 10 days after planting. Seedlings at the other sites were watered only at the time of planting.

At Toolik, both fertilized and control plants were grown in three water treatments, making a 2x3 factorial design for water and fertilizer. To increase water retention (wet treatment), the hole was lined with a piece of 0.05 mm (2 mil) plastic sheeting before the soil was replaced. In the control (mesic) treatment, the original soil was replaced around the seedlings. To decrease water retention (dry treatment), sand from the nearby Atigun

river was substituted for the original soil. Each fertilized seedling received 5 g NPK fertilizer (the same type used in germination experiments) at the time of planting. Treatments were assigned in a randomized complete block design, with 1 replicate of each treatment in each of 20 blocks. The effects of fertilizer and water treatments on growth and leaf nutrient concentrations were examined using 2-way ANOVA. Biomass data were log-transformed, and data on leaf number were square-root transformed. The transformed data within each treatment gave good fits to the normal distribution (Shapiro-Wilk statistic, SAS procedure NORMAL), and variances were homogeneous among the 6 treatments (Levene's test, BMDP 7D). Where ANOVA indicated significant effects of the water treatments, Duncan's multiple comparisons procedure was used to determine which pairs of treatments differed significantly. Numbers of surviving seedlings were compared among treatments using the chi-squared test of independence (Zar 1984).

At the three remote sites where willow seedlings were planted, only the dry and mesic water treatments were used, making a 2x2 factorial design for water and fertilizer. The randomized complete block design was used as at Toolik. Two-way ANOVA was used to determine whether growth of seedlings in the mesic treatment differed among

the remote sites and/or in response to fertilizer. The number of surviving seedlings in the dry treatment was too low to allow analysis of growth data.

Seedlings were harvested near the end of the second season, in August 1986. Because of the loose texture of the soil, it was possible to collect nearly all of the roots. Roots were washed free of soil, and seedlings were divided into root, stem and leaf tissue. Leaves and shoots (live and dead meristems) were counted, and the length of the longest leaf was measured. The tissues were oven-dried at 60^{o}C for approximately 24 hours, then weighed. No further changes in weight of any of the tissues occurred after 24 hours.

Dried leaves of each seedling with > 100 mg of leaf tissue were ground in a Wiley mill, digested in selenous-sulfuric acid and analyzed for N and P using a Technicon autoanalyser (Kedrowski 1983).

Soil analysis

Soil pH, organic matter content and particle size distribution were determined for each of the four transplant gardens. Results are based on 10 samples per site for pH and organic content and 5 samples per site for

particle size distribution except for the Toolik site, where sample sizes were 20 and 10.

Soil organic matter was determined by weight loss on ignition (Jackson 1958). Weighed, air-dry samples (4-7 g) were placed in a muffle furnace for 7 hours at 400°C, then reweighed (Black 1965). Soil particle size distribution was determined by the Bouyoucos specific-gravity method (Gee & Bauder 1986).

RESULTS

Germination

Seeds of Salix alaxensis failed to germinate in glycol solutions with osmotic potentials of -0.5 MPa or lower. Final germination after 10 days did not differ significantly between the control, -0.1 MPa and -0.2 MPa treatments; about 10% of seeds germinated in each (Fig. 3-1). The seeds used in this experiment had been frozen for 10 months, so total germination was much lower than the 90% or higher typical for fresh seeds germinated under optimum conditions. Water content of the top 10 cm of soil of gravel pads ranged from 3.6 to 15.4% of dry weight (Appendix 1). For sandy soils, this corresponds to a range

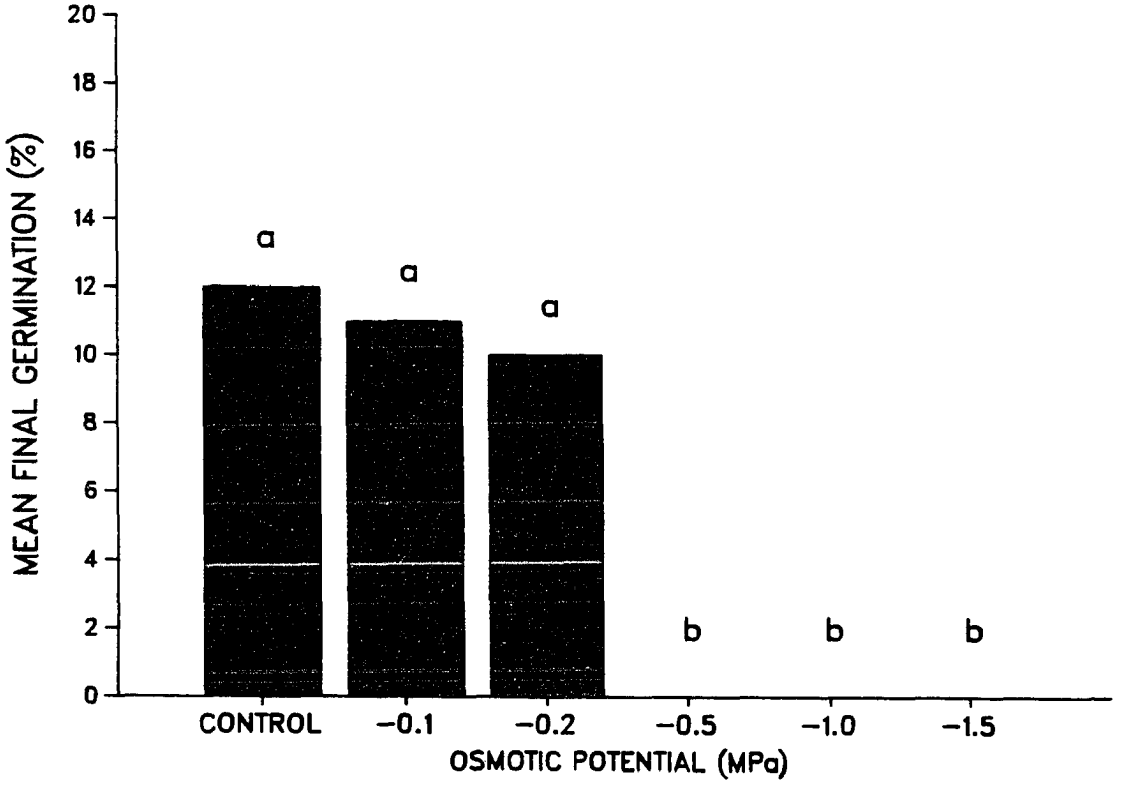

FIG. 3-1. Effects of osmotic potential on germination (after 10 days) of seeds of Salix alaxensis in solutions of polyethylene glycol. Means labelled with the same letter are not significantly different (n = 10). (Kruskal-Wallis test, P > 0.05)

of water potential of approximately -0.01 to -0.3 MPa (Brady 1974). Both water content and water potential are probably lower at the surface due to winnowing of fine particles, making moisture availability limiting for germination of willow seeds.

In pots exposed to ambient temperature and precipitation, germination of fresh seeds was not significantly affected by the interaction between fertilizer and water treatment (Fig. 3-2). The addition of fertilizer reduced germination compared to unfertilized treatments, whether or not water was also added. Watering alone had no significant effect on germination. There were several rainy days during the week this experiment was conducted, which may have weakened any effect of watering.

In field plots, the highest germination percentages (not significantly different from each other) occurred in the plots that were watered regularly and in those to which stones had been added (Fig. 3-3). Germination percentages in all other treatments were significantly lower than in the water and stone treatments, but not significantly different from one another. No germination occurred in plots to which sand or peat had been added. In all treatments where germination occurred, most seeds

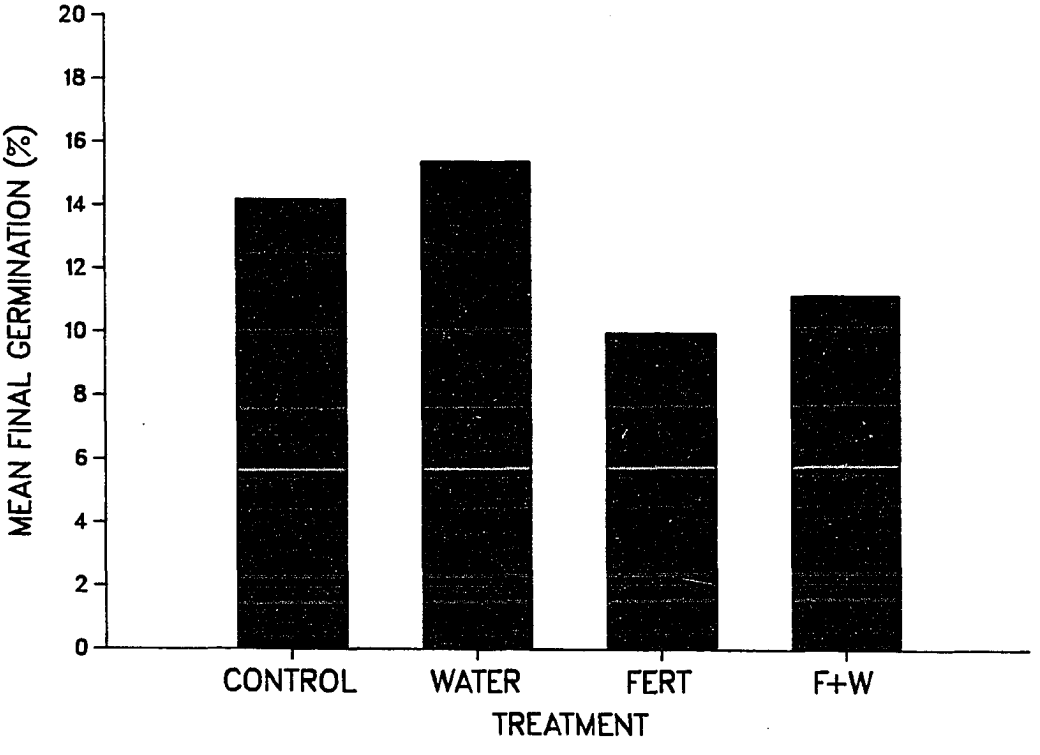

FIG. 3-2. Effects of water and fertilizer treatments on germination (after 5 days) of seeds of Salix alaxensis in pots under field conditions. Fertilizer effect was significant (ANOVA, $P < 0.01$) but water effect and interaction were not ($n = 10$).

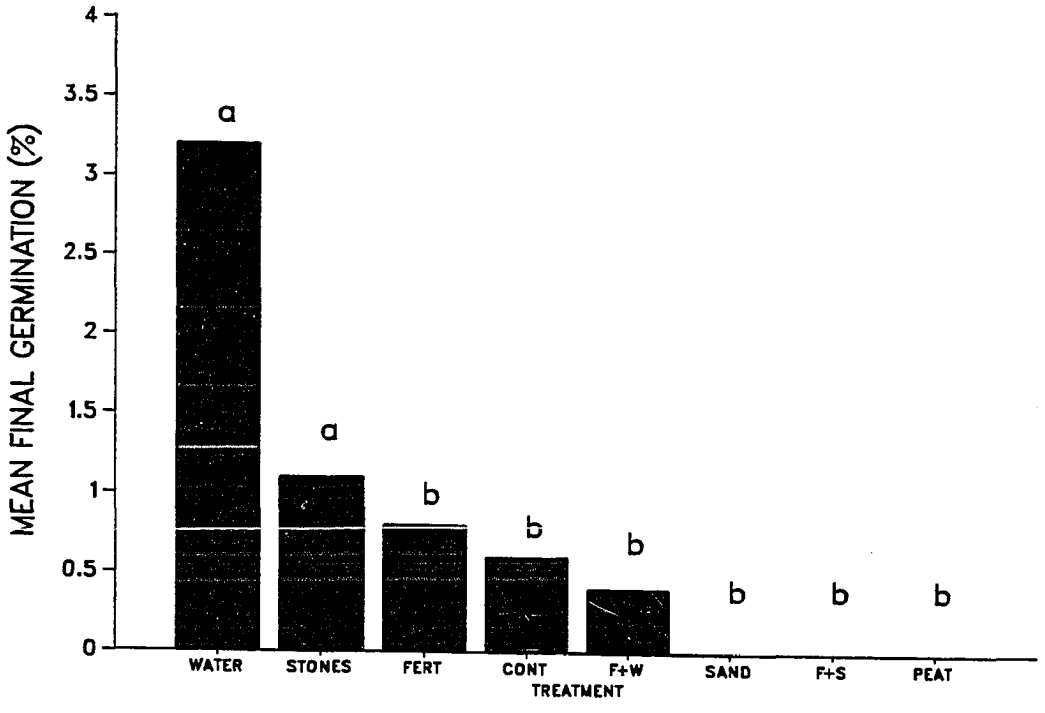

FIG. 3-3. Effects of surface treatments on germination (after 5 days) of seeds of Salix alaxensis in field plots. Means labelled with the same letter are not significantly different (n = 5). (Kruskal-Wallis test, P > 0.05)

germinated near stones, which provided "safe sites" (Harper 1977) protected from the drying effects of wind and sun.

Survival

Survival of transplanted seedlings at Toolik to the end of the second growing season varied from 50 - 85% among nutrient and moisture treatments, but treatment differences were not statistically significant (Table 3-2). At the remote sites, in contrast, survival was much lower in the dry treatment (3 - 5%) than in the mesic treatment (75 - 85%). Seedlings at the remote sites were not watered after planting and failed to establish adequate root systems to survive in the dry treatment. The addition of fertilizer had no significant effect on survival. Sample size was reduced to 10 per treatment at MS 120 by flooding of half the site in spring 1986. Survival could not be assessed at Franklin Bluffs, because hunters camping on the site destroyed an unkown number of seedlings.

TABLE 3-2. Effects of water and fertilizer treatments on survival (to the end of the second growing season) of seedlings of Salix alaxensis transplanted to abandoned gravel pads. Chi-squared statistic indicated significant differences ($P < 0.01$) among treatments at MS 118 and MS 120, but no significant differences at Toolik Lake.

	Number of seedlings surviving		
	Toolik	MS 118	MS 120
Wet			
Control	17	a	a
Fertilized	10	a	a
Mesic			
Control	17	8	16
Fertilized	15	9	14
Dry			
Control	15	1	1
Fertilized	15	0	0
Seedlings planted per treatment	20	10	20
Chi-squared	6.3 ns	27.5 **	14.4 **

a = no seedlings planted

Seedling growth at Toolik

There were no significant interactions between fertilizer and water treatments (Table 3-3), so the main effects of the fertilizer and water treatments could be interpreted clearly from the ANOVA.

Leaf and stem biomass were significantly higher in fertilized seedlings than in controls (Fig. 3-4, Table 3-3), but root biomass was not. Therefore, root:shoot ratio was significantly lower in fertilized seedlings (Tables 3-3, 3-4). The lack of response to fertilizer by roots may reflect the presence of a large amount of root tissue that was produced before the seedlings were transplanted. Decreased root:shoot ratio may also represent a functional response to an increase in nutrient supply. The increased leaf biomass of fertilized seedlings was due mainly to the production of larger, rather than more numerous leaves (Tables 3-3, 3-4). Concentrations of N and P in leaves were higher in fertilized seedlings (Figs. 3-5a, b), indicating that nutrient uptake increased more in response to added nutrients than did growth.

Leaf biomass and number of leaves were significantly lower in the wet than in the dry treatment, while values for the mesic treatment did not differ from either of the others (Fig. 3-4, Tables 3-3, 3-4). Maximum leaf length

TABLE 3-3. Summary of analysis of variance of effects of fertilizer and water treatments on growth and nutrient concentration of seedlings of *Salix alaxensis* transplanted to an abandoned gravel pad (n = 20).

Variable	Source of Var.	df	F ratio	P
Total biomass	Fertilizer	1	6.38	0.014
	Water	2	1.93	0.151
	Interaction	2	1.75	0.181
Leaf biomass	Fertilizer	1	14.32	<0.001
	Water	2	4.06	0.021
	Interaction	2	0.60	0.554
Stem biomass	Fertilizer	1	7.64	0.007
	Water	2	2.74	0.071
	Interaction	2	1.12	0.331
Root biomass	Fertilizer	1	2.27	0.136
	Water	2	1.94	0.150
	Interaction	2	2.41	0.097
Root:shoot ratio	Fertilizer	1	12.59	<0.001
	Water	2	12.31	<0.001
	Interaction	2	1.41	0.250
Leaf number	Fertilizer	1	2.43	0.123
	Water	2	2.63	0.078
	Interaction	2	0.29	0.751
Maximum leaf length	Fertilizer	1	5.18	0.025
	Water	2	3.11	0.050
	Interaction	2	0.40	0.673
Shoot mortality	Fertilizer	1	2.17	0.145
	Water	2	0.48	0.621
	Interaction	2	0.08	0.924
Leaf P concentration	Fertilizer	1	10.12	0.002
	Water	2	1.83	0.167
	Interaction	2	0.88	0.412
Leaf N concentration	Fertilizer	1	25.43	<0.001
	Water	2	0.29	0.752
	Interaction	2	0.28	0.757

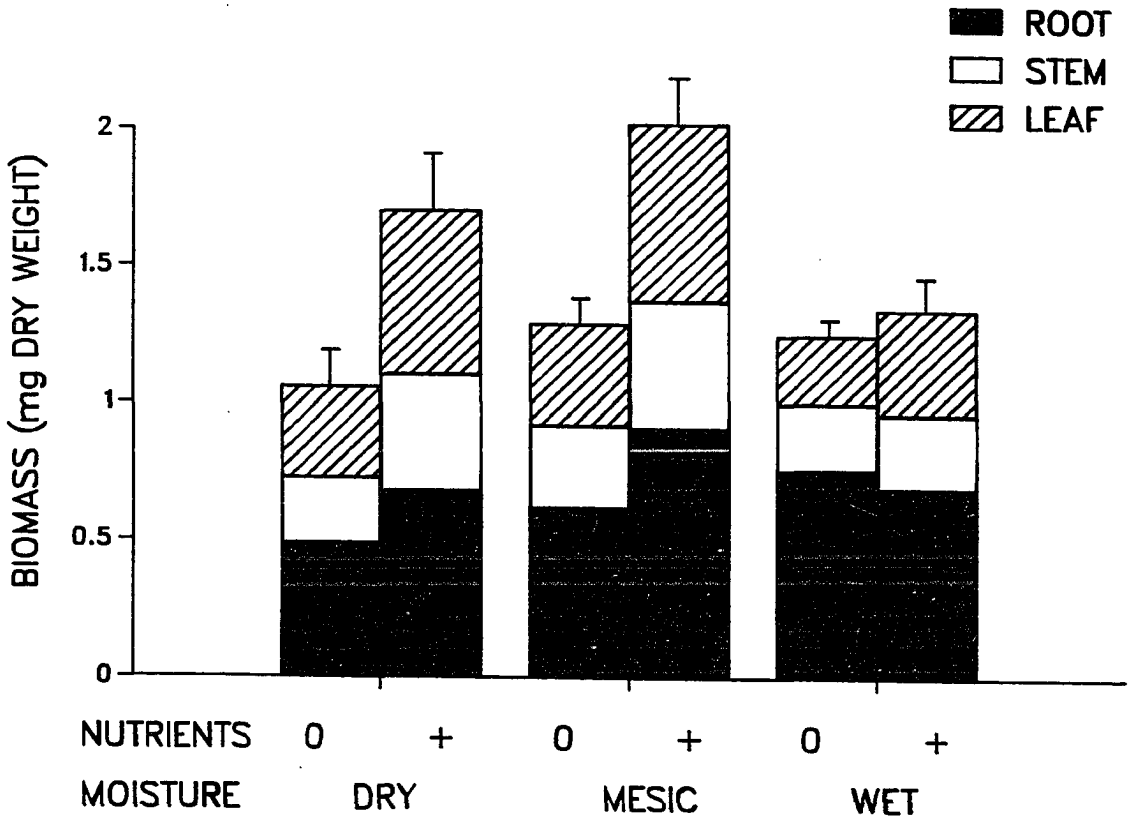

FIG. 3-4. Effects of soil moisture and fertilizer treatments on final biomass of Salix alaxensis seedlings tranplanted to a gravel pad. Statistics are shown in Table 3-4 (n = 20).

TABLE 3-4. Effects of water and fertilizer treatments on components of growth of seedlings of *Salix alaxensis* transplanted to an abandoned gravel pad. Figures are means for treatments. Statistics are shown in Table 3-3.

Treatment	Variable			
	Root:shoot ratio	No. leaves per seedling	Max. leaf length (mm)	% Shoot mortality
Wet Control	1.9	57	31	28
Wet Fertilized	1.1	77	33	21
Mesic Control	1.2	86	40	24
Mesic Fertilized	1.0	93	41	20
Dry Control	1.0	92	33	23
Dry Fertilized	0.7	109	40	16

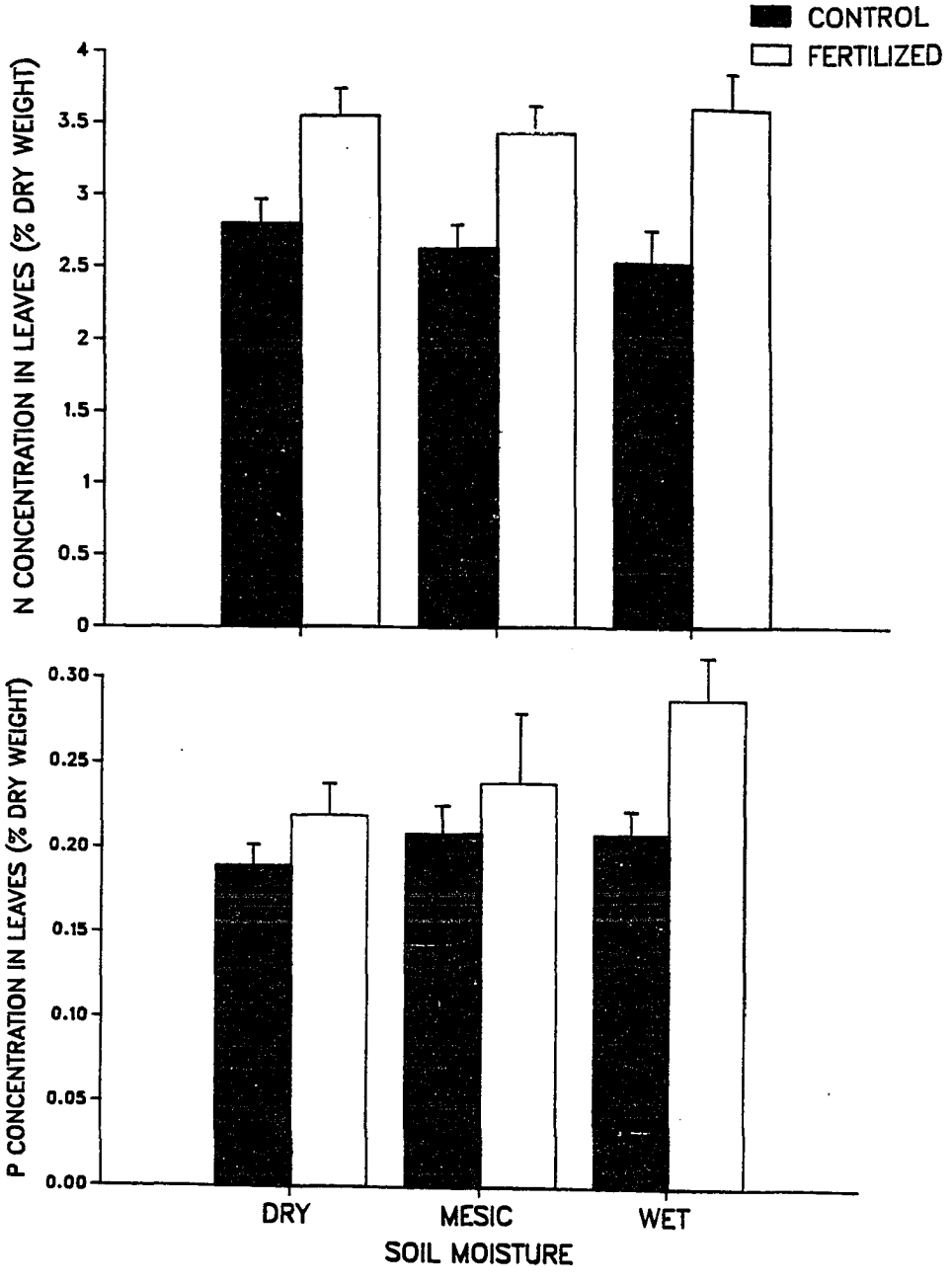

FIG. 3-5. Effects of soil moisture and fertilizer treatments on concentrations of N and P in leaves of transplanted Salix alaxensis seedlings. Statistics are shown in Table 3-4 (n = 20).

was significantly higher in the mesic treatment than in the wet treatment, with intermediate values in the dry treatment. Root:shoot ratio was highest in the wet treatment (Table 3-4), reflecting the reduced leaf growth. Stem biomass and leaf number tended ($P < 0.1$) to be lowest in the wet treatment and highest in the mesic treatment. Overall, there was little difference between the dry and mesic treatments, but both size and number of leaves were significantly reduced in the wet treatment. Possibly the wetter soil remained frozen later in the spring, reducing the effective length of the growing season. Leaf biomass would be most strongly affected, since all of it was produced in the current season.

Seedling growth at remote sites

None of the measured components of growth differed significantly between fertilized and control seedlings (Table 3-5). The number of surviving seedlings with > 100 mg of leaf tissue was insufficient for comparisons of leaf nutrient concentrations among treatments and sites.

Total, root and stem biomass and number of leaves all differed significantly ($P < 0.05$) among the three sites (Table 3-5); leaf biomass tended to differ among sites ($P = 0.09$). Mean values for all biomass components were

TABLE 3-5. Growth and nutrient concentrations of transplanted seedlings of Salix alaxensis on three abandoned gravel pads in northern Alaska. Biomass values are in mg per seedling. Values are means for sites. Means within a row followed by the same letter do not differ significantly.

	Site		
Variable	MS 118	MS 120	Franklin Bluffs
Total biomass	58a	99b	63a
Leaf biomass	14a	20a	13a
Stem biomass	11a	19b	9a
Root biomass	32a	61b	40a
Root:shoot ratio	1.3a	1.7a	1.9a
Leaves (No./seedling)	33a	26ab	19b
Maximum leaf length (mm)	27a	30a	32a
Shoot mortality (%)	27a	26a	35a
Sample size	20	10	20

highest at MS 120, while means for the other two sites did not differ significantly. There were no obvious patterns relating seedling growth to soil characteristics of the gravel pads. Mean values of soil organic matter, water content and content of fine particles were all highest at MS 118 (Table 3-6), but seedling biomass was highest at MS 120 and did not differ significantly between MS 118 and Franklin Bluffs. Soil pH differed among sites, but availability of major nutrients does not vary much over the range observed (6.4 to 7.9).

DISCUSSION

Both water availability and the supply of mineral nutrients limited the establishment of Salix alaxensis on abandoned gravel pads, but the two factors were most important at different stages in the life cycle.

Germination was strongly limited by low availability of water, both in the laboratory and in field plots. Willow seeds are tiny, lose viability within a few days after dispersal (Densmore & Zasada 1983) and have a high moisture requirement for germination (McLeod & McPherson 1972). Seed dispersal of S. alaxensis normally coincides with the retreat of spring floods, so in the riparian

TABLE 3-6. Soil characteristics of abandoned gravel pads where willow seedlings were planted. Values are means for sites ± S.E. Sample sizes for organic matter were 10 at Toolik Lake and 5 for other sites; sample sizes for other variables were 20 at Toolik Lake and 10 at other sites.

	Site			
Variable	Toolik Lake	MS 118	MS 120	Franklin Bluffs
Silt + clay (% dwt)	11 ± 1	23 ± 2	11 ± 2	12 ± 2
Soil pH	7.4 ± 0.2	6.4 ± 0.2	7.5 ± 0.01	7.9 ± 0.01
Organic matter (% dwt)	2.2 ± 0.4	2.9 ± 0.2	2.1 ± 0.5	1.0 ± 0.1
Water (% dwt)	5 ± 0.7	12 ± 0.9	5 ± 0.4	5 ± 0.2

environment seeds can germinate on newly exposed sand and silt (Nechaev 1967; Gill 1971; Argus 1973). Abandoned gravel pads have low water availability in the surface soil, due to lack of fine particles and organic matter. Seeds that land on gravel pads are unlikely to germinate unless the dispersal period of S. alaxensis coincides with a spell of rainy weather. Addition of fertilizer reduced germination, possibly due to osmotic effects reducing water availability.

Unaltered gravel pad material (mesic treatment) supplied enough moisture for survival of seedlings, even when they were only watered at the time of planting. When water holding capacity was reduced (dry treatment) very few seedlings survived except at the site where they were watered during the establishment period. Overall survival in the mesic treatment was approximately 75-80%, similar to the figures reported by Neiland et al. (1981) for seedlings of S. alaxensis transplanted to gravel pads. In the natural riparian environment of S. alaxensis, water supply fluctuates and periods of drought occur. Once rooted, seedlings are apparently able to exploit water when it is available and survive through dry periods.

The growth of established seedlings at Toolik was limited primarily by the availability of nutrients, rather than water. Final biomass, particularly of leaves, was

significantly greater in fertilized seedlings than in controls. Fertilization also increased the growth of transplanted cuttings of S. alaxensis on gravel pads in arctic Alaska (Neiland et al. (1981) and of seedlings in 5 successional stages along the Tanana River in interior Alaska (Walker & Chapin 1986).

In our study, no significant responses to fertilizer were observed at the three remote sites. Because these seedlings were not watered after planting, water stress may have inhibited root growth and/or uptake of the added nutrients. Neiland et al. (1981) found that the response of transplanted cuttings to fertilization varied between gravel pads, and that larger increases in growth occurred on sites where unfertilized cuttings also grew well. The authors suggested that these more favorable sites had higher water availability.

The higher N and P concentrations in leaves of fertilized seedlings indicated that nutrient uptake increased more than did growth in response to increased nutrient supply. This response is typically most pronounced in plants adapted to low-nutrient soils (Chapin 1980) and contrasts with crop plants which generally show a stronger growth response to added nutrients. Neiland et al. (1981) noted that this species occupies a wide range of nutrient regimes, surviving on poor sites but growing

much more rapidly where more nutrients are available. The levels of N and P in leaves of S. alaxensis seedlings in this study were slightly higher than those of cuttings transplanted to gravel pads (Neiland et al. 1981).

Our results suggest that the low cover of willow seedlings on abandoned gravel pads in northern Alaska is primarily due to 1) low numbers of recruits, resulting from lack of moisture for germination (this study) and low seed rain (Chapter 2) and 2) small size resulting from limitation of growth by low nutrient availability. Although most gravel pads were fertilized, much of the nutrient supply is probably tied up in the non-native grasses (now mainly dead) that were sown on the sites (Chapter 2).

Our results indicate that fertilizer is not necessary for survival of established seedlings of S. alaxensis on gravel pads, but can result in significant increases in growth on at least some sites. The soil moisture regime of gravel pads is adequate for survival and growth of established seedlings, but seedlings which do not receive adequate water during the establishment period may fail to respond to added nutrients. The high survival rate of established seedlings is encouraging from the point of view of restoration. Introduction of S. alaxensis to disturbed sites is practical in areas where

lost riparian habitat must be replaced or where shrub cover is desired for esthetic reasons.

ACKNOWLEDGMENTS

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CHAPTER 4

ESTABLISHMENT OF NATIVE LEGUMES ON ABANDONED GRAVEL PADS IN ARCTIC ALASKA[1]

SUMMARY

(1) Revegetation of abandoned gravel pads with non-native grasses has not been successful; alternative approaches using native plants are needed. Legumes are of particular interest because they are important natural pioneers and do not require fertilizer N.

(2) Germination of 4 arctic legumes required scarification of the seed coat, but not stratification. Germination occurred both in light and dark, at both 5°C and 20°C, and was usually over 80%.

(3) Less than 20% of seeds of 2 legume species germinated at water potentials below -0.2 MPa. Such conditions are likely to occur frequently in the surface soil of gravel pads. Under field conditions, germination was increased in moister microsites around stones.

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[1]Susan M. Cargill & F. S. Chapin, III. Submitted to The Journal of Applied Ecology

(4) In the laboratory, total seedling weight was correlated with weight of nodules per plant, but the strength of the relationship declined as availability of mineral N increased.

(5) Rhizobia-free seedlings transplanted to a gravel pad became infected with rhizobia without inoculation, but inoculated seedlings tended to be larger and have a greater weight of nodules per plant.

(6) The high percentage of viable seed, flexible germination requirements, and lack of need for inoculation contribute to the feasibility of using native legumes in restoration of gravel pads. Availability of water for germination may be enhanced by providing microsites with higher water retention.

INTRODUCTION

Raised gravel structures (pads) have been used extensively in arctic regions to prevent thawing of permafrost under roads, camps and work sites. Along the arctic portion of the Trans Alaska Pipeline, most abandoned pads were fertilized and seeded with non-native grasses, but revegetation has not been successful (Van Cleve & Manthei 1972; Kubanis 1980; Chapin & Chapin 1980).

The poor growth and survival of the grasses on gravel pads is attributed to low availability of moisture and nutrients and lack of tolerance to low winter temperatures. Ten years after abandonment, average cover of live grass is only 7% (Chapter 2), and there is no evidence that the sown grass has facilitated invasion by native plants (Neiland et al. 1981; Chapter 2). Successful restoration of gravel pads will depend on approaches using native plants, either direct seeding and planting (Neiland et al. 1981) or encouraging natural invasion (Chapin & Chapin 1980). These approaches will have to be based on an understanding of the natural processes of colonization and succession in the Arctic, and on gravelly sites in particular.

Colonization of abandoned gravel pads in arctic Alaska by native plants has been slow; ten years after abandonment, average cover was 2.7% and average number of species per site was 4.4 (Chapter 2). Legumes in the genera Astragalus, Hedysarum and Oxytropis are prominent in the pioneer community, comprising five of the nine most important colonizing species and contributing approximately 35% of the average total cover of native vascular plants. These species are also common on riparian gravel bars in the area, as are other pioneer species of gravel pads (Chapter 2). Legumes are also important in

early succesion on other nutrient-poor substrates such as glacial outwash (Viereck 1966), gravel exposed by retreating glaciers (Lawrence et al. 1967) and arctic floodplains (Bliss & Cantlon 1957).

Symbiotic associations with N-fixing bacteria (rhizobia) are characteristic of the Leguminosae (Allen & Allen 1981), but both plant and environmental factors affect the extent of the infection and the plant's dependence on it. In particular, either very high or very low availability of mineral N may inhibit nodulation or N fixation (Skeffington & Bradshaw 1981; Sundstrom et al. 1983). Legumes have been recommended for use in revegetation of mine wastes both in North America (Day & Ludeke 1981; Nicholas & McGinnies 1982; Shetron 1983; Shetron & Spindler 1983; Sundstrom et al. 1983) and in Britain (Palaniappan, Marrs & Bradshaw 1979; Jefferies, Bradshaw & Putwain 1981; Jefferies, Willson & Bradshaw 1981). They are less dependent than are other plants on repeated applications of fertilizer, and may contribute N to the soil which can be used by other species (Palaniappan, Marrs & Bradshaw 1979; Jefferies, Bradshaw & Putwain 1981; Jefferies, Willson & Bradshaw 1981). Rhizobia are generally widespread in natural soils, but disturbed soils may lack adequate populations for

seedlings to become infected (Berg 1974; Townsend 1974; Sundstrom et al. 1983).

The objectives of the research reported here were to examine factors limiting the germination of native legumes on gravel pads, to investigate the importance of the symbiotic relationship with rhizobia for the survival and growth of legumes at differing levels of availability of mineral N, and to determine whether the soil of a gravel pad contained a population of rhizobia capable of inoculating transplanted seedlings.

METHODS AND MATERIALS

Study area

The study area was on the North Slope of Alaska, i.e., the area between the crest of the Brooks Range and the Arctic coast. Field experiments were conducted on an abandoned gravel pad at Toolik Lake (68°40' N, 149°40' W). The characteristics of gravel pads and riparian gravel bars in the area are described in Chapter 2). Seeds and nodules of legumes were collected within an area extending approximately 60 km NE from Toolik Lake along the Dalton Highway (formerly known as the North Slope Haul Road).

Stratification and scarification

Scarification and stratification requirements were determined for Oxytropis borealis, O. campestris, Astragalus aboriginum and A. alpinus. Scarified seeds were soaked in concentrated sulfuric acid for either 10 min. or 30 min., and germination was compared with unscarified controls. After scarification, seeds were placed on moist filter paper in Petri dishes, with 20 seeds per dish. The Petri dishes were placed in sealed plastic bags to reduce moisture loss. Five replicates (100 seeds) from each treatment were then placed in a refrigerator (5^{o} C) to stratify. The other 5 dishes from each treatment were placed in a growth chamber in continuous light with a temperature regime of 16 hours at 20^{o}C and 8 hours at 5^{o}C daily. Germination was checked daily and germinated seeds were removed. A seed was considered to have germinated if the radicle had emerged to a length of at least 3 mm. Kruskal-Wallis tests (BMDP 3S) and pairwise comparisons (Conover 1980) were used to determine whether final germination percentages differed among treatments.

Effect of water potential on germination

The response of germination to water availability was examined in the laboratory using solutions of polyethylene glycol 6000 of known water potential. Seeds were scarified for 15 min. in concentrated sulfuric acid and placed in Petri dishes on filter paper moistened with solutions of 0, -0.1, -0.2, -0.5 , -1.0 or -1.5 MPa. Required solution concentrations were calculated according to the formula:

$$Y_s = -(1.18 \times 10^{-2})C - (1.18 \times 10^{-4})C^2 + (2.67 \times 10^{-4})CT + (8.39 \times 10^{-7})C^2T$$

where Ys = water potential of the solution (in bars), C = concentration of the solution (in g PEG kg^{-1} H_2O) and T = temperature (^oC). The Petri dishes were placed in sealed plastic bags and kept in a growth chamber at 20^oC in constant light. Osmotic potential was maintained by weighing the dishes every 2 days and adding distilled water to restore the original weight. Germinated seeds were counted and removed every 2 days for 23 days. Kruskal-Wallis tests followed by pairwise comparisons were used to determine whether final germination percentages differed among treatments.

Seeds which failed to germinate after 23 days were soaked for 30 min. in a 1% solution of tetrazolium chloride and dissected, to determine whether they were still viable. A seed was considered to be viable if both the radicle (including the tip) and the cotyledons stained pink.

Effect of "safe sites" on germination

The effect of "safe sites" (Harper 1977) on germination of Astragalus alpinus was examined in trays (50 cm x 50 cm x 5 cm) of gravel pad material set outdoors at the field station at Toolik Lake. In two diagonally opposite quadrants of each tray, all stones larger than 1 cm in diameter were removed from the surface of the gravel. In the other two quadrants, stones approximately 1 to 5 cm in diameter were added to the surface to cover 50% of the area. Two trays were used per species; seeds scarified for 10 min. in concentrated sulfuric acid were sown in one smooth and one stony quadrant, and unscarified seeds in the other quadrants. This provided a 2 x 2 factorial design for scarification and the effect of a stony vs. a smooth surface. Approximately 100 seeds of A. alpinus or 200 seeds of O. borealis were sown per quadrant. Kruskal-Wallis tests and pairwise comparisons

were used to determine whether the final germination percentage for each species differed significantly among treatments.

Effect of N availability on nodulation

Rhizobia-free seedlings of A. alpinus and O. borealis were grown in the glasshouse from seeds collected in the study area. Seeds were scarified and surface-sterilized by soaking for 10 min. in concentrated sulfuric acid, and placed on moist filter paper in Petri dishes. Germinants were transplanted to sterilized sand in 20 cm^3 "conetainers" (plastic cells used for growing tree seedlings). Different levels of N availability were obtained using Hoagland's solution modified to provide either 1, 10 or 100 ppm of N, while providing all other nutrients at full strength. Seedlings were given 25 ml of nutrient solution once weekly, and distilled water as needed to prevent the sand from drying out.

Seedlings were inoculated at approximately 2 weeks of age, when they had acquired their first true leaves. Seedlings of Phaseolus vulgaris developed more nodules when inoculation was delayed until the seedlings were well established (Sundstrom et al. 1983). Inocula were prepared from nodules collected in the field 6 months previously

and stored frozen. Approximately 5 g of A. alpinus nodules or 3 g of O. borealis nodules were ground in a blender in 300 ml of phosphate-buffered saline. Five ml of the resulting suspension was applied to the sand around the roots of each inoculated seedling. Seedlings of each species received the inoculum prepared from nodules of plants of the same species. Twenty inoculated and twenty control seedlings of each species were grown in each nutrient treatment.

Inoculated and control seedlings were held on the same glasshouse bench. The conetainers were supported in racks, and trays were placed under these in an attempt to minimize contamination of control seedlings with rhizobia. After approximately 4 weeks the seedlings were harvested, divided into root and shoot portions, dried at 60°C to constant weight, and weighed. Nodules were removed before drying, counted, and weighed.

Spearman rank correlation coefficients (BMDP 3S) between weight of nodules and total seedling weight were calculated for each species within each treatment. Kruskal-Wallis tests (BMDP 3S) and multiple comparisons (Conover 1980) were used to determine whether mean weight of nodules per plant differed among N levels for each species.

Nodulation of transplanted seedlings

Rhizobia-free seedlings of *A. alpinus*, *O. borealis* and *O. campestris* were grown in the glasshouse as described above. They were transplanted to the abandoned gravel pad at Toolik Lake in July 1985, when they were approximately 4 months old, 5 to 10 cm tall, and most had produced flowers. When they were transplanted, half the seedlings of each species were inoculated with a suspension of ground root nodules of the same species. The procedure was as described above except that the nodules were freshly collected. Inoculated and control seedlings were planted in separate plots approximately 10 m apart. Seedlings were watered when they were transplanted, but were given no other water and no fertilizer. After 1 year, the seedlings were harvested and the nodules were removed, counted and fresh and dry weights recorded. The plants were divided into shoot and root components, dried and weighed. Mann-Whitney tests (BMDP 3S) were used to determine whether weight of nodules or total seedling weight differed significantly between inoculated and control seedlings of each species.

RESULTS

Stratification and scarification

The effect of stratification on germination could not be determined, as substantial germination occurred while seeds were being cold-treated (Table 4-1). Final germination percentage of unscarified seeds was <5% for all species and both temperature regimes (Table 4-1). Acid scarification for 10 minutes significantly increased germination for all species and both temperatures. Germination percentages for the 30 minute treatment were either slightly higher than those for the 10 minute treatment, or not significantly different.

Effect of water potential on germination

Germination of Oxytropis borealis at -0.1 MPa was the same as in distilled water, but lower water potentials reduced germination significantly compared to the control (Table 4-2). No germination occurred at water potentials below -0.5 MPa. In Astragalus alpinus, germination at -0.1 MPa was significantly lower than in distilled water, and

TABLE 4-1. Final germination percentages (after 9 days) of native legume species after 0, 10 or 30 minutes' scarification in concentrated sulfuric acid. Values are means of 5 replicates of 20 seeds each. Within a row, values followed by the same letter do not differ significantly (Kruskal-Wallis test, $P > 0.05$).

	Germination (% of seeds)		
	Control	10 min.	30 min.
Dark, 5 C			
A. aboriginum	3a	83b	91c
A. alpinus	0a	32b	23b
O. borealis	3a	80b	99c
O. campestris	3a	90b	93c
Light, 20 C			
A. aboriginum	4a	93b	69b
A. alpinus	2a	86b	92b
O. borealis	2a	55b	77c
O. campestris	3a	83b	90b

TABLE 4-2. Germination percentages of scarified seeds of Astragalus alpinus and Oxytropis borealis in solutions of polyethylene glycol of different osmotic potentials. Values are means of 10 replicates of 10 seeds each. Within a column, means followed by the same letter do not differ significantly (Kruskal-Wallis test, $P > 0.05$).

Osmotic Potential of solution	Germination (% of seeds)	
	A. alpinus	O. borealis
0 MPa	96a	65a
-0.1 MPa	71b	60ab
-0.2 MPa	38c	41b
-0.5 MPa	1de	14c
-1.0 MPa	3d	0d
-1.5 MPa	0de	0d

was further reduced at lower water potentials. Less than 1% of seeds germinated at water potentials below -0.5 MPa.

At least 95% of ungerminated seeds of A. alpinus in every treatment contained viable embryos, as did at least 75% of ungerminated O. borealis (Table 4-3). These values were similar to or higher than the final germination percentage for control seeds, indicating that treatment with PEG prevented germination but did not kill the seeds.

Effect of "safe sites" on germination

Germination of both species was significantly higher when stones were added to the gravel surface (Table 3-4). Most germinants were found next to or under the edges of stones, where water evaporated from the soil more slowly. Where no stones were added, germination was 0.1% or less and did not differ significantly between scarified and unscarified seeds. With stones added, between 0.4% and 2.1% of all seeds germinated. Scarification increased germination percentage in A. alpinus and decreased it in O. borealis.

TABLE 4-3. Viability (%) of seeds of Astragalus alpinus and Oxytropis borealis which failed to germinate after 23 days in solutions of polyethylene glycol, at 20 C in continuous light. Numbers of ungerminated seeds examined are shown in parentheses.

Water potential of solution	Seeds still viable (%)	
	A. alpinus	O. borealis
-0.5 MPa	95 (21)	79 (19)
-1.0 MPa	96 (23)	95 (19)
-1.5 MPa	95 (21)	76 (17)

TABLE 4-4. Germination (%) of scarified and unscarified seeds of Astragalus alpinus and Oxytropis borealis in gravel pad material with and without stones added to the surface. Values are means for 5 replicates, of 100 seeds each for A. alpinus and 200 seeds each for O. borealis. Within a column, numbers followed by the same letter do not differ significantly (Kruskal-Wallis test, $P > 0.05$).

	Germination (% of seeds)	
	A. alpinus	O. borealis
Scarified		
Stones present	1.0a	1.0a
Stones absent	0.1b	0b
Unscarified		
Stones present	0.4c	2.1c
Stones absent	0b	0b

Effect of N availability on nodulation

Some control seedlings grown in the glasshouse developed root nodules, indicating infection by rhizobia from the inoculated seedlings. Therefore, control and inoculated seedlings were combined for analysis. Seedling biomass of A. alpinus was significantly correlated with nodule fresh weight at all N levels, but the correlation was strongest (0.85) for seedlings grown at the lowest level of available N (Table 4-5). Mean total dry weight of seedlings increased with the level of available N, but fresh weight of nodules per seedling did not differ significantly among treatments. Thus, the ratio of nodule weight to seedling weight declined with increasing N availability.

In O. borealis, total seedling biomass was significantly correlated with fresh weight of nodules for seedlings given nutrient solution with 1 or 10 ppm N, but not for seedlings grown at 100 ppm N (Table 4-5). The Spearman rank correlation coefficient was highest (0.80) in the lowest N treatment. Mean dry weight of seedlings increased from the lowest to the highest N treatment. Weight of nodules per seedling was significantly lower at 100 ppm N than at 10 ppm N, but did not differ significantly between the two lower N treatments. As in A.

alpinus, the ratio of nodule weight to total seedling weight declined as the availability of N increased.

Nodulation of transplanted seedlings

Most seedlings of all 3 species were flowering at the time they were transplanted and set seed later in the season. Seedlings also flowered and set seed in the following season. In both years, Arctic ground squirrels Spermophilus parryi fed on the flowers and fruits.

After 1 year of growth in the field, both inoculated and control seedlings were nodulated, but mean weight of nodules per plant tended to be higher for inoculated seedlings of all 3 species (Table 4-6). The difference was significant ($P = 0.03$) for O. borealis but not for the other species, possibly because of reduced sample sizes due to seedling mortality. (Seventeen seedlings of O. campestris survived of 23 planted; corresponding figures for A. alpinus and O. borealis were 12/26 and 6/16 respectively.) Similarly, inoculated seedlings tended to be heavier than controls in all species; the difference was significant ($P < 0.05$) in O. campestris, not quite significant in A. alpinus and not significant in O. borealis.

TABLE 4-5. Total dry weight, weight of nodules per plant, and Spearman rank correlation of nodule weight with total seedling weight in Astragalus alpinus and Oxytropis borealis at 3 levels of N availability. Values of nodule weight and seedling weight are means; sample sizes are indicated. Means followed by the same letter did not differ significantly (Kruskal-Wallis test, $P > 0.05$). Significant rank correlation coefficients ($P < 0.05$) are indicated by *.

	Nodule fresh weight (mg)	Seedling dry weight (mg)	r	n
A. alpinus				
1 ppm N	5.9a	13.4a	0.85*	39
10 ppm N	8.7b	37.2b	0.45*	40
100 ppm N	6.7a	138.1c	0.57*	40
O. borealis				
1 ppm N	2.6ab	14.6a	0.80*	18
10 ppm N	3.5a	30.0b	0.49*	31
100 ppm N	1.6b	103.5c	0.11	39

TABLE 4-6. Effect of inoculation with *Rhizobium* on nodulation and growth of transplanted seedlings of *Astragalus alpinus*, *Oxytropis borealis* and *O. campestris* on an abandoned gravel pad. Sample sizes are given in parentheses.

	Dry weight of nodules (mg)	Dry weight of seedling (mg)
A. alpinus		
Control (8)	0.05	1.23
Inoculated (4)	0.08	2.04
Mann-Whitney test statistic	2.34	2.88
Significance level	0.13	0.09
O. borealis		
Control (3)	0.10	3.74
Inoculated (3)	0.12	5.63
Mann-Whitney test statistic	0.43	0.43
Significance level	0.51	0.51
O. campestris		
Control (10)	0.07	3.09
Inoculated (7)	0.11	4.38
Mann-Whitney test statistic	4.49	3.70
Significance level	0.03	0.05

DISCUSSION

Establishment of native legumes on abandoned gravel pads is likely to be limited by lack of available water for germination. Water content of the top 10 cm of gravel pads has been estimated at 4 - 15% of dry weight (Chapter 2). In sandy soils, this is equivalent to a range of water potential of approximately -0.01 to -0.3 MPa (Brady 1974). On the soil surface, where fine particles are lacking and evaporation is more rapid, water potential is probably often -0.5 MPa or lower. Under these conditions, germination of A. alpinus and O. borealis is likely to be limited by lack of moisture, except where stones on the surface provide microsites with lower evaporation rate.

In laboratory tests, very few seeds of Astragalus aboriginum, A. alpinus, Oxytropis borealis or O. campestris germinated without scarification. Soaking seeds for 10 minutes in concentrated sulfuric acid was an effective scarification treatment. In the natural environment, the seed coat may be broken by repeated freeze-thaw cycles, or by abrasive action of sand. Stratification was apparently not required by these species. Light and temperature requirements were not highly specific; all species showed some germination at both 5°C in the dark and and 20°C in continuous light.

Total germination percentages for most species/treatment combinations were > 80%, indicating a high percentage of viable seed.

Growth of seedlings in the laboratory was positively correlated with weight of nodules per plant, with the strongest correlations at the lowest availability of mineral N. Symbiotic N fixation apparently contributed significantly to seedling growth, but the importance of the contribution declined as the availability of mineral N increased. This suggests that the presence of rhizobia is required for establishment of legumes in nutrient-poor disturbed soils, although not necessarily in more fertile soils.

In the laboratory, weight of nodules per seedling of O. borealis was reduced at the highest availability of mineral N, suggesting that use of excessive fertilizer in revegetation could inhibit infection of roots by rhizobia. High availability of mineral N can also reduce N fixation by established nodules. N fixation by white clover Trifolium repens was not affected by fertilizer inputs of 50 kg N ha^{-1}, but was clearly reduced by inputs of 200 kg N ha^{-1}. (Skeffington & Bradshaw 1980). In snap beans Phaseolus vulgaris grown on mine soil, nitrogenase activity was inhibited by 50 kg ha^{-1} or more of N (Sundstrom et al. 1983).

Both inoculated and control seedlings transplanted to a gravel pad formed nodules, but inoculated seedlings tended to have higher total biomass and greater weight of nodules per plant. Rhizobia capable of infecting these legume species were evidently present in the soil of the gravel pad, but the population densities may have been low enough to limit the extent of infection. The response of seedling dry weight to inoculation indicated that growth was N-limited, and that fixation by the rhizobia was a significant source of N for the seedlings. Sundstrom et al. (1983) reported that P. vulgaris grown on Virginia mine soil did not form nodules unless inoculated. Caragana arborescens, a leguminous shrub, formed few nodules and grew poorly in field trials on disturbed soil in New Zealand, but both nodulation and growth were significantly improved by inoculation (Wills 1982).

The available evidence suggests that relationships between arctic legumes and their rhizobia are not highly specific. Strains of rhizobia isolated from 3 arctic legumes, Astragalus alpinus, Oxytropis maydelliana and O. arctobia, were able to inoculate all 3 species (Prevost et al. 1987). Rhizobia present in disturbed soils in the Arctic would probably be effective with many or all native species of the closely related genera Astragalus and Oxytropis.

Native legumes are attractive candidates for use in restoration of gravelly disturbed sites in arctic Alaska for a number of reasons, including considerations of wildlife needs and esthetics, as well as their ability to thrive without expensive N fertilizers. For the species we examined, percentage of viable seed was high and germination requirements with respect to light and temperature were flexible. Availability of water is likely to limit germination under field conditions; this could be ameliorated somewhat by a rough surface providing moister microsites for germination. Inoculation with rhizobia may not be needed; at least on the gravel pad we studied, enough rhizobia were present in the soil for seedlings to become infected. However, in situations where rapid establishment was required, inoculation with appropriate rhizobia might increase seedling growth. It would probably not be necessary to use different inocula for each species (Prevost et al. 1987).

Seedlings of A. alpinus, O. borealis, and O. campestris flowered and set seed in the first season, suggesting that cover could increase quite rapidly from a modest initial planting. Legumes do invade gravel pads naturally, but invasion limited by disperal distance from riparian seed sources (Chapter 2). On sites where rapid recovery is desired, sowing or transplanting legumes could

establish the nucleus for a self-sustaining plant community.

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CONCLUSIONS

Development of tundra restoration techniques using native species will require understanding of the natural processes of colonization and succession operating in the Arctic. On abandoned gravel pads, the naturally-occurring pioneer community is dominated by species normally associated with riparian gravel bars, including willows Salix alaxensis and S. glauca, fireweed Epilobium latifolium, horsetails Equisetum variegatum and legumes of the genera Astragalus, Oxytropis and Hedysarum. Both total cover and diversity of native plants were inversely correlated with distance from seed sources in the riparian zone. Legumes, with relatively heavy seeds, were more restricted to sites near the river than were willows and fireweed with their light, wind-dispersed seeds.

Establishment of S. alaxensis on gravel pads is probably limited by the availability of both water and nutrients, but at different stages in the life cycle. Very few seeds germinated at moisture potentials typical for gravel pads, but germination was improved somewhat on a rough surface that provided moister microsites. The growth

of established seedlings was not limited by water availability on a gravel pad, but was limited by nutrient availability. Seedling survival was high and apparently not limited by either the moisture or nutrient regime of the gravel pad.

The availability of water in gravel pad soils probably also limits the germination of legume (Astragalus and Oxytropis) seeds. Provision of a rough surface with shaded microsites significantly improved germination. Seedlings transplanted to a gravel pad formed root nodules without inoculation, indicating that at least in this case the soil contained a population of Rhizobia. However, there was some indication that inoculated seedlings formed more nodules and grew faster.

The low cover and diversity of native plants on 10-year old abandoned gravel pads is attributed to 1) limitations of disperal from seed sources on riparian gravel bars, 2) limitation of germination by low water availability and 3) limitation of growth, especially of non-legumes, by low availability of N and other mineral nutrients.

Transplanting seedlings of S. alaxensis would be a feasible option for restoration where shrubs are required to replace lost wildlife habitat or for esthetic reasons. An initial application of fertilizer would be useful in

increasing early growth, but repeated application should not be necessary for survival. Sowing willow seed is unlikely to be successful because of the high moisture requirement for germination and short period of seed viability.

Legumes are attractive candidates for use in restoration because their capacity for symbiotic N fixation eliminates the need for costly N fertilizers. They may also contribute N to the soil which can be used by other species. Sowing legume seed on gravel pads might be feasible if adequate "safe sites" for germination were provided. Transplanting seedlings should be practical for sites where more rapid cover is required. Inoculation might improve growth, but would probably not be necessary.

The failure of attempts to revegetate gravel pads with introduced grasses does not mean that it is impossible to restore these sites. Some native plants adapted to riparian gravel bars (a similar substrate) are quite capable of growing on gravel pads if obstacles to dispersal and germination are overcome. Alternative approaches to restoration can be developed, based on the use of native species and understanding of natural processes of invasion and community development.

APPENDIX 1

Table A1: Location, vegetation and soil characteristics of Site 1 (Toolik Runway) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 68°40'N Longitude = 149°50'W

Distance from Sagavanirktok River = 12 km.
Road distance from Prudhoe Bay = 206 km.

Species	Family	Cover (%)
Epilobium latifolium	(Onagraceae)	2.8
Oxytropis nigrecens	(Leguminosae)	0.4
Dryas integrifolia	(Rosaceae)	0.2
Carex bigelowii	(Cyperaceae)	0.2
Salix spp. (glauca)	(Salicaceae)	0.1
Equisetum arvense	(Equisetaceae)	0.1
Epilobium angustifolium	(Onagraceae)	TR
Salix alaxensis	(Salicaceae)	+
Crepis nana	(Compositae)	+
Stellaria sp.	(Caryophyllaceae)	+
Eriophorum angustifolium	(Cyperaceae)	+
Saxifraga tricuspidata	(Saxifragaceae)	+
Potentilla fruticosa	(Rosaceae)	+
Total cover of native species		3.6
Total cover of non-native (seeded) grass		6.7
Live cover of non-native grass		2.7
Dead cover of non-native grass		4.0

Table A1, cont.

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	37 ± 2.0
Organic matter (% soil dwt)	(10)	2.1 ± 0.2
Water content (% soil dwt)	(10)	13 ± 1.0
Sand (% of < 2mm fraction)	(5)	87 ± 1.4
Silt (% of < 2mm fraction)	(5)	8 ± 1.2
Clay (% of < 2mm fraction)	(5)	4 ± 0.5
Soil pH	(10)	7.1 ± 0.1

Table A2: Location, vegetation and soil characteristics of Site 2 (Kuparuk Material Site) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 68°40'N Longitude = 149°38'W

Distance from Sagavanirktok River = 15 km.
Road distance from Prudhoe Bay = 200 km.

Species	Family	Cover (%)
Equisetum arvense	(Equisetaceae)	1.1
Total cover of native species		1.1
Total cover of non-native (seeded) grass		45
Live cover of non-native grass		11
Dead cover non-native grass		34

Note: Only the gravelly, peripheral part of the site was examined. The central area, where overburden had been dumped, had substantial cover of Epilobium angustifolium, Achillea borealis and other herbs.

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	49 ± 1.7
Organic matter (% soil dwt)	(10)	3.2 ± 0.1
Water content (% soil dwt)	(10)	5 ± 0.2
Sand (% of < 2mm fraction)	(5)	85 ± 0.7
Silt (% of < 2mm fraction)	(5)	10 ± 0.5
Clay (% of < 2mm fraction)	(5)	5 ± 0.4
Soil pH	(10)	7.4 ± 0.1

Table A3: Location, vegetation and soil characteristics of Site 3 (APL 117-1) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 68°41'N Longitude = 149°10'W

Distance from Sagavanirktok River = 8 km.
Road distance from Prudhoe Bay = 189 km.

Species	Family	Cover (%)
Salix spp. (glauca)	(Salicaceae)	+
Astragalus alpinus	(Leguminosae)	+
Epilobium angustifolium	(Onagraceae)	+
Saxifraga punctata	(Saxifragaceae)	+
Total cover of native species		+
Total cover of non-native (seeded) grass		53
Live cover of non-native grass		7
Dead cover non-native grass		46

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	63 ± 2.7
Organic matter (% soil dwt)	(10)	1.8 ± 0.3
Water content (% soil dwt)	(10)	15 ± 1.8
Sand (% of < 2mm fraction)	(5)	86 ± 1.0
Silt (% of < 2mm fraction)	(5)	9 ± 0.6
Clay (% of < 2mm fraction)	(5)	6 ± 0.7
Soil pH	(10)	7.3 ± 0.03

Table A4: Location, vegetation and soil characteristics of Site 4 (MS 118) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 68°41'N Longitude = 149°08'W
Distance from Sagavanirktok River = 5.5 km.
Road distance from Prudhoe Bay = 187 km.

Species	Family	Cover (%)
Oxytropis nigrescens	(Leguminosae)	0.4
O. borealis	"	+
O. campestris	"	+
O. mertensiana	"	+
Astragalus eucosmus	"	+
Salix pulchra	(Salicaceae)	+
Total cover of native species		0.4
Total cover of non-native (seeded) grass		64
Live cover of non-native grass		9
Dead cover non-native grass		55

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	41 ± 1.6
Organic matter (% soil dwt)	(10)	2.9 ± 0.2
Water content (% soil dwt)	(10)	12 ± 0.9
Sand (% of < 2mm fraction)	(5)	77 ± 0.5
Silt (% of < 2mm fraction)	(5)	13 ± 0.9
Clay (% of < 2mm fraction)	(5)	9 ± 0.6
Soil pH	(10)	6.4 ± 0.2

Table A5: Location, vegetation and soil characteristics of Site 5 (Slope Mountain MS) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 68°43'N Longitude = 149°01'W

Distance from Sagavanirktok River = 5 km.
Road distance from Prudhoe Bay = 181 km.

Species	Family	Cover (%)
Total cover of native species		0
Total cover of non-native (seeded)	grass	26
Live cover of non-native grass		8
Dead cover non-native grass		26

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	33 ± 0.8
Organic matter (% soil dwt)	(10)	4.9 ± 0.3
Water content (% soil dwt)	(10)	4 ± 0.3
Sand (% of < 2mm fraction)	(5)	78 ± 2.6
Silt (% of < 2mm fraction)	(5)	14 ± 1.6
Clay (% of < 2mm fraction)	(5)	8 ± 1.0
Soil pH	(10)	7.6 ± 0.1

Table A6: Location, vegetation and soil characteristics of Site 6 (Accomplishment Creek) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 68°43'N Longitude = 148°57'W

Distance from Sagavanirktok River = 4 km.
Road distance from Prudhoe Bay = 179 km.

Species	Family	Cover (%)
Epilobium latifolium	(Onagraceae)	0.1
Equisetum arvense	(Equisetaceae)	0.1
Oxytropis borealis	(Leguminosae)	0.1
O. campestris	"	0.1
Astragalus aboriginum	"	+
A. alpinus	"	+
A. eucosmus	"	+
Dryas integrifolia	(Rosaceae	+
Total cover of native species		0.4
Total cover of non-native (seeded) grass		70
Live cover of non-native grass		15
Dead of cover non-native grass		55

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	40 ± 1.0
Organic matter (% soil dwt)	(10)	1.7 ± 0.1
Water content (% soil dwt)	(10)	4 ± 0.2
Sand (% of < 2mm fraction)	(5)	85 ± 1.0
Silt (% of < 2mm fraction)	(5)	9 ± 0.7
Clay (% of < 2mm fraction)	(5)	5 ± 0.5
Soil pH	(10)	7.7 ± 0.1

Table A7: Location, vegetation and soil characteristics of Site 7 (MS 120-1) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 68°49'N Longitude = 148°48'W

Distance from Sagavanirktok River = 0.1 km.
Road distance from Prudhoe Bay = 165 km.

Species	Family	Cover (%)
Astragalus alpinus	(Leguminosae)	1.3
Salix spp. (glauca)	(Salicaceae)	0.9
Lupinus arcticus	(Leguminosae)	0.6
Oxytropis borealis	"	0.4
Equisetum arvense	(Equisetaceae)	0.4
O. campestris	(Leguminosae)	0.1
S. alaxensis	(Salicaeae)	0.1
Hedysarum alpinum	(Leguminosae)	0.1
H. mackenzii	"	0.1
Shepherdia canadensis	(Eleagnaceae)	0.1
Senecio sp.	(Compositae)	0.1
Epilobium latifolium	(Onagraceae)	0.1
Astragalus alpinus	(Leguminosae)	+
A. eucosmus	"	+
Dryas integrifolia	(Rosaceae	+

Total cover of native species	4.3
Total cover of non-native (seeded) grass	54
Live cover of non-native grass	8
Dead of cover non-native grass	45

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	33 ± 4.8
Organic matter (% soil dwt)	(10)	1.5 ± 0.1
Water content (% soil dwt)	(10)	5 ± 0.4
Sand (% of < 2mm fraction)	(5)	82 ± 1.7
Silt (% of < 2mm fraction)	(5)	11 ± 0.6
Clay (% of < 2mm fraction)	(5)	6 ± 1.1
Soil pH	(10)	7.9 ± 0.01

Table A8: Location, vegetation and soil characteristics of Site 8 (MS 120-2A) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 68°51'N Longitude = 148°49'W

Distance from Sagavanirktok River = 0.1 km.
Road distance from Prudhoe Bay = 163 km.

Species	Family	Cover (%)
Astragalus alpinus	(Leguminosae)	2.9
Equisetum arvense	(Equisetaceae)	2.6
H. mackenzii	(Leguminosae)	1.3
Oxytropis borealis	"	1.0
Hedysarum alpinum	"	0.2
A. eucosmus	"	0.2
Senecio sp.	(Compositae)	0.1
Salix alaxensis	(Salicaceae)	TR
S. spp. (*glauca*)	"	+
Lupinus arcticus	(Leguminosae)	+
A. aboriginum	"	+
Stellaria sp.	(Caryophyllaceae)	+
Shepherdia canadensis	(Eleagnaceae)	+
Epilobium angustifolium	(Onagraceae)	+
Arctostaphylos sp.	(Ericaceae)	+
Parnassia kotzebuei	(Saxifragaceae)	+
Pedicularis sp.	(Scrophulariaceae)	+
Total cover of native species		8.3
Total cover of non-native (seeded) grass		58
Live cover of non-native grass		7
Dead of cover non-native grass		51

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	no data
Organic matter (% soil dwt)	(10)	2.1 + 0.5
Water content (% soil dwt)	(10)	5 ± 0.4
Sand (% of < 2mm fraction)	(5)	89 ± 1.8
Silt (% of < 2mm fraction)	(5)	7 ± 1.3
Clay (% of < 2mm fraction)	(5)	4 ± 0.6
Soil pH	(10)	7.5 ± 0.01

Table A9: Location, vegetation and soil characteristics of Site 9 (MS 120-2B) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 68°52'N Longitude = 148°49'W

Distance from Sagavanirktok River = 0.1 km.
Road distance from Prudhoe Bay = 163 km.

Species	Family	Cover (%)
Equisetum arvense	(Equisetaceae)	1.1
Astragalus aboriginum	(Leguminosae)	0.4
Salix spp. (*glauca*)	(Salicaceae)	0.2
Oxytropis campestris	(Leguminosae)	0.2
Lupinus arcticus	"	0.2
O. borealis	"	0.1
Astragalus alpinus	"	0.1
A. eucosmus	"	+
Salix alaxensis	(Salicaceae)	+
Epilobium latifolium	(Onagraceae)	+

Total cover of native species	2.4
Total cover of non-native (seeded) grass	34
Live cover of non-native grass	5
Dead of cover non-native grass	29

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	45 ± 1.1
Organic matter (% soil dwt)	(10)	1.0 ± 0.03
Water content (% soil dwt)	(10)	10 ± 0.4
Sand (% of < 2mm fraction)	(5)	91 ± 0.7
Silt (% of < 2mm fraction)	(5)	5 ± 0.6
Clay (% of < 2mm fraction)	(5)	4 ± 0.2
Soil pH	(10)	7.5 ± 0.02

Table A10: Location, vegetation and soil characteristics of Site 10 (MS 121-1) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 68°53'N Longitude = 148°51'W

Distance from Sagavanirktok River = 0.2 km.
Road distance from Prudhoe Bay = 160 km.

Species	Family	Cover (%)
Equisetum arvense	(Equisetaceae)	1.3
Oxytropis borealis	(Leguminosae)	0.6
Salix spp. (glauca)	(Salicaceae)	0.5
Crepis nana	(Compositae)	0.3
Astragalus alpinus	(Leguminosae)	0.1
A. aboriginum	"	0.1
Dryas integrifolia	(Rosaceae)	0.1
Potentilla fruticosa	"	+
Oxytropis campestris	(Leguminosae)	+
Lupinus arcticus	"	+
Hedysarum alpinum	"	+
H. mackenzii	"	+
A. eucosmus	"	+
Salix alaxensis	(Salicaceae)	+
Epilobium latifolium	(Onagraceae)	+
Arctostaphylos sp.	(Ericaceae)	+
Senecio sp.	(Compositae)	+
Saussurea angustifolia	"	+
Castilleja elegans	(Scrophulariaceae)	+
Stellaria sp.	(Caryophyllaceae)	+
Shepherdia canadensis	(Eleagnaceae)	+

Total cover of native species	3.0
Total cover of non-native (seeded) grass	37
Live cover of non-native grass	9
Dead of cover non-native grass	29

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	36 ± 1.5
Organic matter (% soil dwt)	(10)	1.0 ± 0.02
Water content (% soil dwt)	(10)	3 ± 0.3
Sand (% of < 2mm fraction)	(5)	92 ± 0.5
Silt (% of < 2mm fraction)	(5)	4 ± 0.7
Clay (% of < 2mm fraction)	(5)	4 ± 0.3
Soil pH	(10)	8.0 ± 0.02

Table A11: Location, vegetation and soil characteristics of Site 11 (Kakukturat Mtn.) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 69°01'N Longitude = 148°49'W

Distance from Sagavanirktok River = 0.1 km.
Road distance from Prudhoe Bay = 142 km.

Species	Family	Cover (%)
Equisetum arvense	(Equisetaceae)	7.0
Oxytropis borealis	(Leguminosae)	0.7
Astragalus alpinus	"	0.3
Hedysarum alpinum	"	0.3
H. mackenzii	"	0.3
Salix spp. (*glauca*)	(Salicaceae)	TR
Total cover of native species		8.6
Total cover of non-native (seeded) grass		27
Live cover of non-native grass		4
Dead of cover non-native grass		23

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	41 ± 1.6
Organic matter (% soil dwt)	(10)	1.1 ± 0.1
Water content (% soil dwt)	(10)	3 ± 0.3
Sand (% of < 2mm fraction)	(5)	85 ± 1.4
Silt (% of < 2mm fraction)	(5)	10 ± 0.9
Clay (% of < 2mm fraction)	(5)	5 ± 0.6
Soil pH	(10)	7.7 ± 0.01

Table A12: Location, vegetation and soil characteristics of Site 12 (Lupine River) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 69°08'N Longitude = 148°51'W

Distance from Sagavanirktok River = 0.2 km.
Road distance from Prudhoe Bay = 128 km.

Species	Family	Cover (%)
Equisetum arvense	(Equisetaceae)	0.9
Salix spp. (glauca)	(Salicaceae)	0.1
Total cover of native species		1.0
Total cover of non-native (seeded) grass		55
Live cover of non-native grass		8
Dead of cover non-native grass		47

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	30 ± 3.5
Organic matter (% soil dwt)	(10)	1.3 ± 0.2
Water content (% soil dwt)	(10)	2 ± 0.3
Sand (% of < 2mm fraction)	(5)	84 ± 2.0
Silt (% of < 2mm fraction)	(5)	10 ± 1.4
Clay (% of < 2mm fraction)	(5)	6 ± 0.8
Soil pH	(10)	7.8 ± 0.02

Table A13: Location, vegetation and soil characteristics of Site 13 (Dan Creek) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 69°10'N Longitude = 148°49'W

Distance from Sagavanirktok River = 0.1 km.
Road distance from Prudhoe Bay = 126 km.

Species	Family	Cover (%)
Equisetum arvense	(Equisetaceae)	4.3
Salix spp. (glauca)	(Salicaceae)	1.4
S. alaxensis	"	0.7
Epilobium latifolium	(Onagraceae)	0.5
Arctagrostis latifolia	(Gramineae)	0.4
Oxytropis borealis	(Leguminosae)	0.2
Total cover of native species		7.5
Total cover of non-native (seeded) grass		0
Live cover of non-native grass		0
Dead of cover non-native grass		0

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	43 ± 1.4
Organic matter (% soil dwt)	(10)	0.9 ± 0.1
Water content (% soil dwt)	(10)	5 ± 0.7
Sand (% of < 2mm fraction)	(5)	88 ± 1.6
Silt (% of < 2mm fraction)	(5)	8 ± 1.0
Clay (% of < 2mm fraction)	(5)	4 ± 0.4
Soil pH	(10)	7.7 ± 0.01

Table A14: Location, vegetation and soil characteristics of Site 14 (Happy Valley Runway) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 69°10'N Longitude = 148°49'W

Distance from Sagavanirktok River = 0.2 km.
Road distance from Prudhoe Bay = 126 km.

Species	Family	Cover (%)
Salix spp. (glauca)	(Salicaceae)	0.6
S. alaxensis	"	0.3
Crepis nana	(Compositae)	0.2
Equisetum arvense	(Equisetaceae)	0.1
Epilobium latifolium	(Onagraceae)	0.1
Dryas integrifolia	(Rosaceae)	0.1
Hedysarum mackenzii	(Leguminosae)	TR
H. alpinum	"	+
Oxytropis borealis	"	+
O. campestris	"	+
Astragalus eucosmus	"	+
Carex bigelowii	(Cyperaceae)	+
Shepherdia canadensis	(Eleagnaceae)	+
Arctostaphylos sp.	(Ericaceae)	+
Senecio sp.	(Compositae)	+
Saxifraga oppositifolia	(Saxifragaceae)	+
Total cover of native species		1.4
Total cover of non-native (seeded) grass		0
Live cover of non-native grass		0
Dead of cover non-native grass		0

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	41 ± 2.1
Organic matter (% soil dwt)	(10)	1.3 ± 0.2
Water content (% soil dwt)	(10)	5 ± 0.7
Sand (% of < 2mm fraction)	(5)	87 ± 1.8
Silt (% of < 2mm fraction)	(5)	10 ± 1.7
Clay (% of < 2mm fraction)	(5)	3 ± 0.5
Soil pH	(10)	7.8 ± 0.01

Table A15: Location, vegetation and soil characteristics of Site 15 (Franklin Bluffs Camp) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 69°44'N Longitude = 148°20'W

Distance from Sagavanirktok River = 0.2 km.
Road distance from Prudhoe Bay = 58 km.

Species	Family	Cover (%)
Oxytropis borealis	(Leguminosae)	1.1
Hedysarum mackenzii	"	0.3
O. campestris	"	0.2
Total cover of native species		1.6
Total cover of non-native (seeded) grass		34
Live cover of non-native grass		16
Dead of cover non-native grass		18

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	47 ± 1.2
Organic matter (% soil dwt)	(10)	1.0 ± 0.1
Water content (% soil dwt)	(10)	5 ± 0.2
Sand (% of < 2mm fraction)	(5)	88 ± 1.2
Silt (% of < 2mm fraction)	(5)	8 ± 1.1
Clay (% of < 2mm fraction)	(5)	4 ± 0.2
Soil pH	(10)	7.9 ± 0.01

Table A16: Location, vegetation and soil characteristics of Site 16 (Coastal Plain) in 1986. TR = cover < 0.1%, + = species observed on site but not on transects.

Latitude = 69°45'N Longitude = 148°20'W

Distance from Sagavanirktok River = 0.1 km.
Road distance from Prudhoe Bay = 56 km.

Species	Family	Cover (%)
Oxytropis borealis	(Leguminosae)	0.2
Hedysarum alpinum	"	0.1
Astragalus alpinus	"	0.1
A. eucosmus	"	0.1
Artemisi tilesii	(Compositae)	0.1
Total cover of native species		0.6
Total cover of non-native (seeded) grass		8
Live cover of non-native grass		1
Dead of cover non-native grass		7

Soil characteristic	(n)	Mean ± S.E.
Rocks (% total dry weight)	(10)	48 ± 0.9
Organic matter (% soil dwt)	(10)	1.0 ± 0.02
Water content (% soil dwt)	(10)	5 ± 0.4
Sand (% of < 2mm fraction)	(5)	91 ± 1.1
Silt (% of < 2mm fraction)	(5)	6 ± 0.7
Clay (% of < 2mm fraction)	(5)	3 ± 0.5
Soil pH	(10)	8.0 ± 0.02

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